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AN ENQUIRY INTO THE ANALYTICAL MECHANISM OF THE INTERNAL EAR

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TORONTO

AN ENQUIRY INTO THE ANALYTICAL MECHANISM OF THE INTERNAL EAR

BY

SIR THOMAS WRIGHTSON, Bart.

MEMB. INST. C.E.

WITH AN APPENDIX
ON THE ANATOMY OF THE PARTS CONCERNED
BY

ARTHUR KEITH, M.D., F.R.S.

MACMILLAN AND CO., LIMITED
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PREFACE

The conversion of sound waves into auditory stimuli has always been clouded with mystery.

Mathematicians and physicists have carried their investigations into the method by which, in the case of air, sound can be carried by wave action to the ear, but there is very little exact physical or anatomical knowledge of the route and method by which these wave actions reach the auditory nerves.

The Germans have assumed that the vibrations of sound through the cochlea are transmitted on the principle of resonance. This view has of late years been received with decreasing favour by anatomists and physiologists.

Since Helmholtz gave his sanction and support to this solution of the problem, a vast amount of anatomical and physiological knowledge has been brought to light bearing upon the mechanism of our sensory organs.

The principal critics of the Helmholtz hypothesis are found among the anatomists, who fail to see the possibility of the basilar membrane vibrating in a liquid, and so preserved in tension and weight for a lifetime as to move in resonance to tones varying from say thirty vibrations to six or eight thousands per second.

For many years I have been interested in this problem and given much time to its study, and long ago I came to the conclusion that I could not hope to make progress unless associated in the work with an expert anatomist.

In Dr. Arthur Keith I found one who recognised all the difficulties of the problem and who gave me the greatest encouragement to go on with the inquiry. In fact, had it not been for his unstinted help I could never have put forward the case which is presented in this treatise, which, without any claim to be a final solution, may, I hope at all events, be regarded as an alternative to the resonance theory.

Forty years ago, when studying the wave forms of compound tones and the harmonic curves from which they are built up, I found it necessary to design and make an instrument which at one and the same time could produce two separate harmonic sine curves and immediately contiguous (and therefore most easily comparable) the compound wave form arising from them, which with my mechanism is automatically produced.

The crests and hollows of the simple tones are equidistant and therefore periodic, each according to its vibration rate, but in the compound wave the crests and hollows are no longer equidistant. The compound wave form may be of almost infinite variety if either the amplitudes or the relative phases of the two original vibrations be altered.

After making great numbers of compound diagrams I at last found, by actual measurements, that—although the distance apart of crests and hollows was no longer equal—if the crossing points of the compound curve on the axis were regarded as impulse points as well as the maxima and minima of the crests and hollows, there were revealed to the eye numerous systems of consecutive impulses which not only satisfied the requirements of individual frequency for the simple tones, but also systems of impulses which were necessary to produce the differential and summational tones.

This observation is the basis of the argument presented in this publication.

The problem to be determined was whether these impulses are preserved and carried forward in the liquids of the cochlea to the termination of the auditory nerves, and what relation the to and fro motions at the stapes have to the motions at these nerve terminations.

In a preface it is not always wise to anticipate the main argument, but it may be well to indicate that in resonance it is not only necessary for the original vibrator and the resonator to have elastic properties, but that the medium through which the wave forms pass should also be highly elastic. This is not the case after the motion of the air is transferred at the stapes into the liquids of the cochlea. The new medium is (at the minute pressures dealt with) inelastic and incompressible, and will therefore be moved instantaneously in the passages of the cochlea as each increment of pressure in the air wave acts through the ossicles upon the stapes.

Although resonance acts in producing the motion up to this point, we have to look to other agencies for the further conveyance of the motion and impulses through the liquid.

These agencies are, according to this theory, the displacement of the liquid in the cochlea and the movements of the basilar membrane as affected by the areas of the passages.

These movements are *dead beat* in their character, being controlled by the constancy of the liquid volume and its incompressibility, and further modified by the resistances of certain elastic bodies which introduce subjective changes in the wave-form of the liquid in the cochlea. Under these conditions the motion of the stapes can be accurately conveyed with the steadiness of a hydraulic machine to the nerve terminals, provided the mechanical arrangements are suitable.

This is where an engineer's experience and an anatomist's knowledge may come in, and in my share of the investigation my endeavour has been to follow the sequence of every change of pressure and displacement in the liquid particles between the stapes and the nerve terminations.

T. WRIGHTSON.

1st February, 1917.

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ANALYTICAL MECHANISM OF THE INTERNAL EAR

CHAPTER I

HARMONY AND THEORY OF IMPULSES DESCRIBED

In the course of a somewhat busy life I have devoted a good deal of my leisure to the study of acoustics. As an amateur musician my attention was especially drawn to the *raison d'être* of harmony and the study of compound wave forms and their graphic representations.

As an engineer I was familiar with the action of the steam engine indicator, an instrument which records the varying pressures of the steam as it acts upon the piston, and which, when transferred into a graphic diagram, shows to the eye the actual useful work which the steam is accomplishing. It also reveals indications of defects in the admission of the steam, and any impulses due to defective construction or losses of power due to the cooling of the steam on expansion. If by means of a steam indicator diagram the work of the steam and the impulses generated could be usefully analysed, it seemed reasonable to argue that a similar analysis could be expected in the case of diagrams which correctly indicated the pressures, velocities, and impulses of sound waves.

Sir John Herschel's definition of harmony was as follows: "The sense of harmony depends upon the periodical recurrences of coincidental impulses on the ear, and affords perhaps the only instance of a sensation, for whose pleasing impression a distinct intelligible reason can be assigned."

My search was for the indication of these recurrent impulses in the diagram which represented the wave form of a sound, simple or compound according to their form as demonstrated by the investigations of mathematicians.

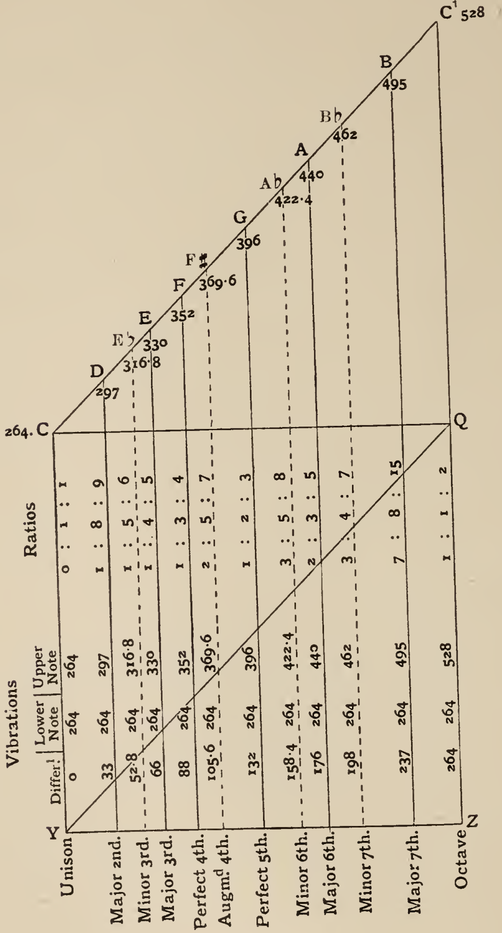
C' 528
B 495
B♭ 462
A 440
A♭ 422·4
G 396
F♯ 369·6
F 352
E 330
E♭ 316·8
D 297
264. C
Q
Y
Z
Ratios
Vibrations
Differ.
Lower Note
Upper Note
Unison 0 264 264 0 : 1 : 1
Major 2nd. 33 264 297 1 : 8 : 9
Minor 3rd. 52·8 264 316·8 1 : 5 : 6
Major 3rd. 66 264 330 1 : 4 : 5
Perfect 4th. 88 264 352 1 : 3 : 4
Augmd 4th. 105·6 264 369·6 2 : 5 : 7
Perfect 5th. 132 264 396 1 : 2 : 3
Minor 6th. 158·4 264 422·4 3 : 5 : 8
Major 6th. 176 264 440 2 : 3 : 5
Minor 7th. 198 264 462 3 : 4 : 7
Major 7th. 237 264 495 7 : 8 : 15
Octave 264 264 528 1 : 1 : 2

FIG. 1.

In 1876 I published my views of that time.[1] In this first chapter I shall record the graphic method I then employed. There is nothing in this early paper which contradicts the conclusions I subsequently came to, but the methods later employed are more in accord with the actual calculations of mathematicians, and, in order to render these accurately graphic, special machinery for constructing sine curves and their combinations was designed which I will describe in a later chapter.

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[1] President's Address on Phenomena of Sound, Cleveland Inst. Engineers, April 10, 1876.

I have designed the diagram Fig. 1 with the view of showing graphically the position of the various consonant intervals. The base line $Y\ Z$ represents 0 vibration per second; the horizontal line $C\ \ Q$ represents a tone of 264 vibrations (middle C of the piano), its vertical distance from $Y\ Z$ being laid down to a scale of 264 units of length. A second note, represented by the line $C\ C^1$ is supposed to rise gradually through all the positions of the gamut to the note C^1 of 528 vibrations, or double that of the lower note. This note we may call the octave above the lower note. If we keep the lower note sounding uniformly, while we make the second note gradually rise through all the positions, we may represent the changing effect by supposing a vertical line, $Z\ C^1$ to move horizontally across the paper, and, commencing at the left hand of the diagram, we shall find that, after leaving the position $Y\ C$ which represents unison, the imaginary vertical line when it arrives at position E will be intersected in such a way by the lines $C\ Q$ and $C\ C^1$ that the division will be in the aliquot proportion of 4 : 5, and on testing the corresponding notes on the syren we shall find the interval of a third, in which every fifth crest of one set of waves corresponds with every fourth crest of the other, and we experience the sensation of harmony. Moving on our vertical line, we come to position F, in which it is intersected in the proportion of 3 : 4. This interval is called the perfect fourth. At G we find the intersection in the proportion of 2 : 3, corresponding to a perfect fifth, and so on, as figured on the diagram, for all the intervals up to the octave where the proportion is as 1 : 2. The "periodical recurrence of coincidental impulses" is most easily discerned when the integral ratio is the simplest, and expressed by the smallest figures, and, therefore, the octave (1 : 2) is the most harmonious interval, then the fifth (2 : 3), next the perfect fourth (3 : 4), then the major third and major sixth (4 : 5 and 3 : 5 respectively), then the minor third (5 : 6), and so on until we come to the major seventh (8 : 15), which is the most inharmonious of all those included in the gamut.[1]

A little reflection will show that with the almost infinite number of different ratios of wave-lengths which you could compound in the way I have described you would produce an infinite number of different wave forms, all of which could be, as it were, decomposed into the original wave forms. But on looking at these compound forms, we feel that there is no recognition on the part of the eye of the original simple wave forms. Professor Helmholtz has proposed the hypothesis of an analytic power possessed by the ear by which that organ can analyse the compound wave into its original constituents. Now if we can possibly see in the compound wave form indications of effect which correspond to the various phenomena of compound sounds, we shall be on the high road to discover what is the nature of this unexplained analytic power.

We know that, in the indicator diagram of a steam engine, the vertical pressure line is quite an arbitrary length, depending upon the strength of the spring; and we can in the case of the pulsation diagram of a sound wave in air increase the height of the ordinates representing the pressure and velocity without lengthening the distance from crest to crest of the wave.

---

[1] We must here draw a distinction between the terms harmonious and melodious. The former refers to isolated effects of two or more notes sounded together, whereas the latter refers to effects produced by notes following each other in melody. In harmony the interval of a fifth is very nearly as perfect as that of an octave, but in melody consecutive fifths are execrable. Again, consecutive thirds in melody are pleasant, although, harmonically speaking, they are not such perfect intervals as fifths. In melody, considerations of tonal relationship come into play which do not exist in the harmony of isolated chords. A neglect of this consideration has frequently led musicians to differ from scientific men in the relative order of harmoniousness in the various intervals, but when the distinction between the terms harmonious and melodious is fully recognised, there should be no difference of opinion between art and science.

The higher the vertical ordinates are carried, the nearer will your wave diagram approach to the form of a triangle, and the great English philosopher, Dr. Young, one of the first who investigated the waves of sound, generally represented them in this manner.

In his "Experiments and Inquiries respecting Sound and Light," published in his Biography, by Dr. Peacock, late Dean of Ely, he says, "to simplify the statement let us suppose what probably never precisely happens, that the particles of air in transmitting pulses proceed and return with uniform motion." He then goes on to show graphically, by means of straight lines instead of curves, the waves of sound. By following this plan we can readily obtain the compound effect of any number of co-existent pulsations. On Plate 1 at end of book I have shown a number of combined forms of two simple notes.

The first phenomenon of compound sounds which we will consider is the fact that when two or more different sets of periodic vibrations enter the ear the sensation of each tone is perfectly distinct. When we consider the number of distinct pulsations of air which must vibrate in the small aperture to the ear in listening to the performance of a large orchestra, from which our ears receive numerous waves varying from 25 feet to three or four inches in length, and when, after allowing for all this, we know that we can also at the same time hear other less musical sounds, such as the rustling of dresses, the whispers of some of the audience, and, frequently, the distant sounds of the street outside the concert-room, the mind is oppressed with the complication of the problem, and is almost tempted to retire from its contemplation in despair.

I will, however, try to reduce it to one of its simplest forms, by showing how several musical tones may be supposed capable of being heard without confusion.

In order to prepare your minds for the consideration,

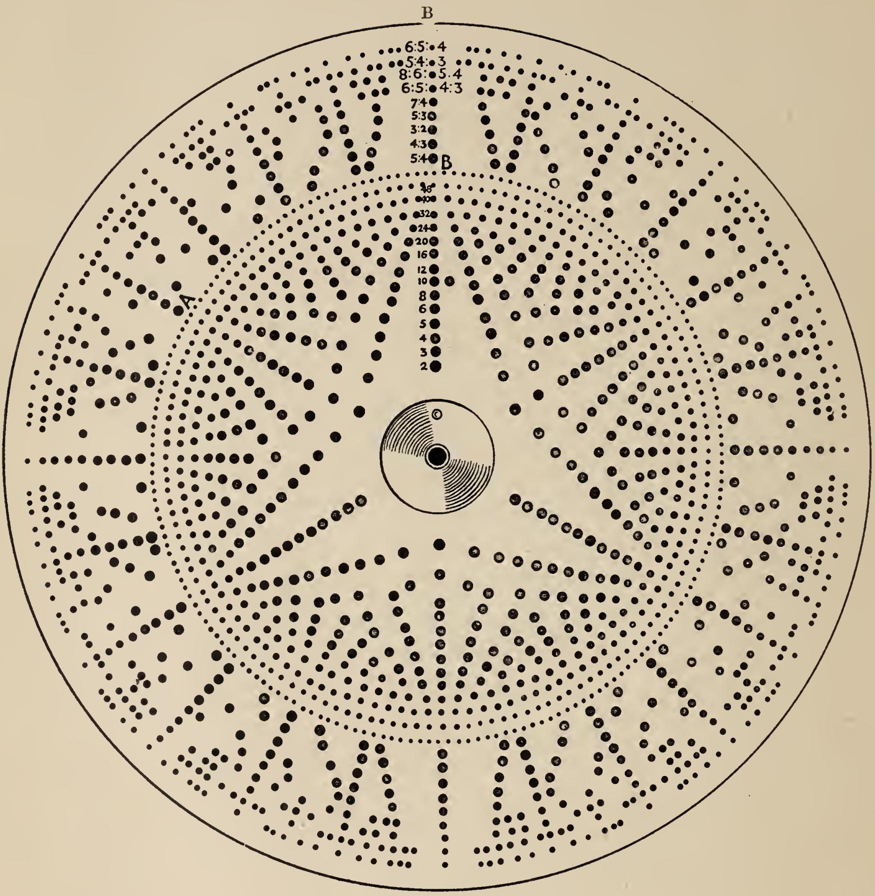

Fig. 2.

I will describe an instrument called a Seebeck's Syren, which illustrates the principle upon which musical sounds are produced. In the original instrument (see Fig. 2), a series of equidistant holes punched in a circle on a disc is made to revolve, while a stream of air is directed against the holes through a small pipe. As each hole passes, the air goes through it with a puff which forms a pulse in the stratum of air on the other side. The passing of the holes at regular speed makes the successive pulsations periodic. Hence the musical tone heard when the instrument is blown. As the circles of holes approach the centre, the number passing the pipe in a given time is less, consequently the note is lower, and by arranging the holes properly you can with a uniform speed of rotation produce all the notes of the gamut upon this instrument. Now what I have described is the instrument in its simplest and original form ; but I wish you *particularly to notice* an extension of the principle.

Outside the regular holes I have described, you will see circles of holes which appear very irregular in their distance apart, but which are really each composed of two, three, or four systems of holes. For instance, in the first circle the space *A B* is divided off into, first, four spaces and then into five spaces, and the same all round the circle.

Now, if when the disc is rotating we blow through a quill upon this double series of holes, we shall find that, although the distances between each consecutive hole are not equal, and that, therefore, in this respect they do not comply with the requirement of frequency, yet we absolutely hear two distinct notes, each corresponding to its series 4 and 5, and clearly sounding the musical interval called a major third ; in other words, that the ear recognises the individual frequency of each system of puffs, and that one does not interfere with the other. Take the outer row of holes, where there are three systems in the proportion of 6 : 5 : 4. On causing the disc of the syren to revolve, and blowing, we get a chord composed of notes the vibration numbers of which are in the above ratio. The third and fourth circles of holes from the edge of the syren are divided off, each into four systems of holes, viz., 4, 5, 6, 8, and 3, 4, 5, 6, and on blowing we hear a faint chord of four notes corresponding to the vibration rates.

At intervals of time corresponding with the consecutive distance of the holes there will doubtless be an inward movement of the membrane of the ear, the outward movement following immediately on the rarefaction of the pulse. These vibrations of the membrane, although not consecutively periodic, are each in their individual system periodic. This appears to be sufficient to enable us to recognise each individual tone, in spite of the apparent confusion presented to the eye in examining the various circles of holes. The amazing delicacy of the elastic action of the air is wonderfully exemplified in considering this remarkable phenomenon, and its wondrous character is intensified when we remember that it is not only two or three notes, but many systems of vibrations, the individuality of which the ear is capable of distinguishing.

The next phenomenon of compound sounds we will consider is the well-known sensation of beats. On the wind chest of a pair of acoustic bellows suppose we have two organ pipes of nearly the same length, which when sounded give the notes E and F, having respectively 330 and 352 vibrations per second. Now if by artificially lengthening the F pipe the pitch of its tone is lowered, until it very nearly coincides with that of the E pipe ; a beating sound will now be distinctly heard, very slow when the difference of the length in the pipes is very small, and increasing in rapidity as the difference of length becomes greater, until at last the beats are so rapid that they cease to be distinguishable. This peculiar phenomenon is due to what is called interference, which, shortly explained, is as follows. Suppose the vibrations of the upper pipe to be 331 per second, while the lower pipe gives 330, then once in every second it is evident that the crests of one set of waves entering the ear will correspond with the crests of the other set of waves, and that once in each second the crests of one set will be neutralised by the hollows of the other set; the compounding, therefore, of the two sets of waves will have a maximum and minimum effect each second. If we make a difference of two vibrations in a given time, we shall have, in that given time, two reinforcements of sound called beats. A practical rule has been derived from these observations, that the number of beats per second is always equal to the difference of the number of vibrations per second in the primaries. Dr. Pole, in an interesting article which appeared in *Nature*, January 13th and 20th, 1876, shows that this rule is not absolutely correct, and instances a case where the number of vibrations are 100 and 103 per second respectively. Here the first vibration of each will coincide exactly, and the last of each also, but the thirty-third vibration of one will occur after 33/100ths of a second, and the thirty-fourth vibration of the other after 34/103rds of a second, and as these fractions are not the same, it is clear the vibrations will not coincide exactly, neither will the sixty-sixth and sixty-eighth; in fact, there will be only one point in each second when the vibrations will coincide. But in rapid vibrations, such as we have in musical tones, the effect of beats is produced not only when the absolute coincidences occur, but also when we have near approaches to coincidences, such as described. Hence the rule given is practically correct for notes within what is called beating distance.[1]

Now if we turn to our diagrams (Plate I at end of book) we shall detect the phenomenon of beats very distinctly shown. Take the case of notes very near each other, say, in the proportion of 4 : 5, and we shall find that all the figures with a ratio the difference of which is 1 have the same character. If we look at 15 : 16, we can easily see that 100 : 101 will have the same character, although the number of vibrations will be greater in the whole cycle of change. In all these cases we see that the motion transmitted to the drum of the ear passes from a maximum to a minimum in each cycle of change.

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[1] This rule is of great practical value for tuning instruments, as by the beats the tuner can know when his unisons are in perfect tune. He can further tell when his fifths are in tune, from the fact that the third harmonics of the lower note and the second harmonic of the upper note will beat, as can be illustrated on the organ pipes.

Now take ratios with a difference of two; 3 : 5 and 5 : 7 (Plate I) are examples of these. You will see defined periods of maximum and minimum effect, two occurring in each cycle of change, though the two from absolute coincidence not happening are not exactly equal in effect, as pointed out by Dr. Pole, and before him by Dr. Young, and so the mind argues at once that, make the number of vibrations as much larger as we like, the same character of alternations will hold good. 4 : 7 and 5 : 8 show examples of beat with a difference of three. We may therefore assume that this phenomenon of beats is fully accounted for in our graphic method by the periodic rising and falling of intensity in pressure on, and consequent motion of, the drum skin of the ear.[1]

Let us now take another phenomenon of compound sounds, viz., differential tones. These are also called Tartini's tones, from a great Italian violinist who first noticed them. Returning to our experimental organ, if the two notes C and G (the interval of a perfect fifth) were sounded, on listening attentively, in addition to each of the primary tones, a deep note can be distinguished, exactly an octave below C. Now C has 264 double vibrations per second, and G 396, and we shall find that the differential tone has 396 − 264, or 132 vibrations. This tone is called the differential tone, because its vibration number is equal to the difference of the vibration numbers of the primaries. Again, take the interval of a perfect fourth, say C upwards to F. On sounding these notes you distinctly hear a note which is an octave and a fifth below the lowest note or two octaves below the highest. This note has a vibration number of 88 per second, the primaries C and F being respectively 264 and 352, difference = 88. If we examine all the other musical intervals we shall find the same holds good; the closer the prime notes are together the deeper the differential tone.

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[1] From these considerations it appears that the beating of tones is principally due to periodic variations in amplitude.

As I shall have to return more fully to consider the question of these tones with relation to harmony, it is very desirable that we should fully realise their effects. I therefore draw your attention again to Fig. 1, page 2, which illustrates graphically the effect of resultant tones.

Now we shall find that as the sliding upper note arrives at the position *D*, of 297 vibrations, a deep note at almost the limit of audibility, having 297 – 264, or 33 vibrations per second, is heard. Rising with the upper note to E of 330 vibrations, a differential tone of 330 – 264 = 66 is heard. Sound G and 396 – 264 or 132 is heard, and so on. If we now set off these differential tones to scale, measuring as before from the base line, we shall find that the corresponding points all lie in the straight line *Y*, *Q*, which is parallel to *C*, C^1, and that they rise from 0 to 264 vibrations per second, while the upper primary rises from 264 to 528.

The next phenomenon of compound sounds is one which has been discovered by that distinguished German philosopher, Professor von Helmholtz. He calls it the summational tone. As may be inferred from the name, this tone has a vibration number equal to the sum of the vibration numbers of the primaries. Helmholtz states that "it is generally very much weaker in sound than the differential tone and is to be heard with decent ease, almost only on the harmonium and the polyphonic syren."[1] He also states that many of the summational tones form extremely inharmonic intervals, with their generators, and that were they not generally so weak on most instruments they would give rise to intolerable dissonances. Being very weak, and difficult to make audible, their existence perhaps does not affect consonance to any great extent, but the phenomenon ought to be accounted for in the diagrams, if my graphic method be correct.

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[1] Ellis's translation of Helmholtz's "Tonempfindungen," p. 234.

I have now described to you the phenomena which are made known to our senses in the sounding of two simple tones of different vibrations.

We have, first, the fact that each tone is heard distinctly and entirely unaffected by the other;

Secondly, the phenomenon of beating when the notes are nearly in unison or consonance;

Thirdly, that of differential tones;

Fourthly, that of summational tones.

Now my proposition is that for every one of these sensations of compound sound transmitted to the ear we should find a corresponding indication in our diagram if the system of graphic representation be correct.

First, as to the individual clearness of the two prime tones. We find that each apex of the wave, representing the prime tones, has its corresponding apex in the compound diagram.

These apices in the compound figure may be blunter, or may vary in other ways from those in the single figures, but in every case there is a decided change of direction in the compound figure corresponding exactly in time with a change of direction of each of the single figures. Now the compound figure represents the advancing and retreating motion of the inner membrane of the ear. Of course the motion of a point in the centre of this membrane moves backwards and forwards in a straight line, but it moves along this line at varying velocities, the centre of the line of travel being represented by the normal position of the membrane. When this membrane advances and is then brought to a momentary standstill, as it would be at a moment of time corresponding to any of the sharp points of the compound diagram, an impulse of change of velocity and of momentum will be projected in the liquid inside the labyrinth of the ear upon the auditory nerves, producing a sensation on the brain; when the drum skin is retreating and comes to a stop, an impulse of change of velocity and momentum will also pass to the nerves, and the brain will receive a sensation. Even when the compound only shows a blunt point, the motion continuing but at a slightly altered velocity, as shown in the diagram by a change in direction, this will produce an impulse representing change in velocity and momentum of the drum skin.

We should then have thrown upon the auditory nerves a series of impressions following each other in exactly the same sequence of time as the changes occur in the two single waves of tone. Now these impressions appear to be exactly similar in effect to those given by the Seebeck's syren, where, with two or more series of impressions in the shape of puffs of air, it was shown that one series of impressions did not interfere with the other, but that each produced its proper tone, and the same reasoning should hold good in considering a greater number of simple tones sounding.

Secondly, as to beats. I think enough has been said to show that the representation of the beats is, in the rise and fall of intensity of sound, clearly shown in the diagrams, the rise and fall appearing most equable in the case where the lowest integral ratio of the single notes has a difference of one.

Thirdly and fourthly. As to differential and summational tones, I take the two together, as, judging from these diagrams (Plate I), they appear to be due to the same cause. Looking at the compound diagrams, where there is a difference of one in the aliquot proportion of the simple tones, when the wave diagram is in phase, that is, when the waves start together, two crests coinciding, as in proportion 2 : 3, it is evident that once in each cycle of vibrations exactly the same impression is produced: that is, while one tone makes two and the other three vibrations there will be one recurrence of phase in each complete cycle of change, one being the difference between two and three. The same is readily seen in all the other cycles where a difference of one exists, and where the crests coincide once in each cycle; but, as a matter of fact, the crests need not necessarily start together, and probably rarely do. Von Helmholtz has shown experimentally that varying phase does not at all affect the quality of the combined tone, although the shape of the compound wave may be very different.[1] When the waves are out of phase, definite effects, corresponding with the phenomenon of the differential tone, are not so evident, but a little examination will reveal what we search for. The dotted horizontal line represents in all these compound figures the zero of pressure or the normal position of rest of the vibrating membrane of the ear.

Now, as an illustration of the argument, imagine a kettledrum filled with liquid right up to the drum skin, and that this skin is suddenly pressed in by the hand, say one-fourth of an inch, below the plane of rest, and suppose that there is an elastic membrane in the lower part of the kettledrum which will allow the displacement to find relief. The sudden one-quarter inch depression in the drum skin will bring a considerable and sudden tension on the skin, which will pull inwards the ring of the kettledrum, and impart to the liquid in the drum a converging wave. Now, suppose the indentation of one-fourth of an inch be allowed to return, and that a force should continue the motion of the skin to a position one-fourth of an inch above the plane of rest, then the ring of the drum will again be drawn inwards, and a second converging wave produced. When the drum skin was at its central position the drum sides would be at their greatest extension, and a moment's reflection will show that for each time the kettledrum skin passes the central position you will have obtained a complete to and fro horizontal vibration of the ring or sides which, with the kettledrum full of liquid, would throw a converging wave to the centre of the instrument. Now, apply this reason to the motion of the inner drum skin of the ear. In our compound diagram of the two pure tones we find numerous crossings of this central position, and on examination of many diagrams in all kinds of phases I have found that the distance is so proportioned that they fully account for the existence both of the differential and the summational tones.[1] We will take a few examples from the diagrams. In the case of the proportion of 5 : 7, which is the interval known by musicians as the augmented fourth (see Plate I), we find altogether fourteen points where the membrane of the ear would, in following the condensation and rarefaction of the air, pass the central position, and, on measurement, I find that the following twelve points are all equidistant, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 1, 2, etc. Points 1 *D* and 2 *D* are still left unaccounted for, and appear to be inserted in a very arbitrary way amongst the equal divisions already named; but on measuring their distances we find that the points 1 *D*, 2 *D*, 1 *D*, etc., are exactly equidistant, and that therefore there is an equal recurrence of impressions 1 *D*, 2 *D*, 1 *D*, etc., going on without interfering with the more rapidly recurring impressions first mentioned. We have already shown, experimentally, by the disc syren, that separate systems of impressions produce independent tones, and we may therefore expect it to be so in this case. The more rapid impressions, twelve in number (5 plus 7), correspond with the summational tone first observed by Helmholtz. The slower impressions, two in number (7 minus 5), correspond with the differential tones first noticed by Tartini. Examine 7 : 10 — 11 : 15 — 8 : 13 — 7 : 13 (see Plate I), or any other ratio, and you will readily recognise the same effect. Further, an alteration of phase does not affect the result (see diagrams) which show ratios of 4 : 7 and 5 : 7, in various altered phases, the equidistance of the crossing points remaining a feature of the composite figure, however much the contour of the figure be varied, owing to the alteration of phase. Now examine the diagrams where aliquot proportions have a difference of 3. Take, for example, 5 : 8 (Plate I), the interval known as a minor sixth. Here we have fifteen positions where the membrane of the ear would pass the neutral line ; of these, on measurement, we shall find 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 1, 2, etc., equidistant and therefore producing the summational tone of 5 plus 8 = 13 ; and we also find the following points 1 *D*, 2 *D*, 3 *D*, 1 *D*, etc., giving three equidistant points in each cycle (one of which, viz., 2 *D*, coincides in this particular phase with point 7 in the other system). These produce the differential tone due to 8 − 5 = 3 impressions, while the prime tones are making respectively 8 and 5. Examine in the same way 4 : 7, a musical minor seventh, or the unmusical intervals 7 : 10, 8 : 13, 11 : 15, 7 : 13, and we find in every case the same differential tone, but a much higher summational tone. Vary the phase, and the same equidistant crossing points are discovered.

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[1] "Tonempfindungen," Ellis's translation, p. 186.

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[1] It will be shown later that through the resistances of the elastic muscles known as the tensor tympani and the stapedius also through similar resistances in the motion of the basilar membrane there is a suspension of pressure velocity and momentum as the membrane passes its central position. This will cause the impulses at that position to be greatly emphasised in definition.

An objection might now be raised that this does not account for the much greater intensity in the differential compared with the summational tones. I account for this by the same effect in rising and falling in intensity, occurring in the case of the beats, also occurring with greater rapidity in the production of differential tones. If you notice the diagrams, the crossing point of the differential tone is in each case at the minimum sound of the beating effect. At the crossing points, therefore, the distinct impressions are created which are filled in between with the beating phenomenon we have described. There are, however, no definite points at the maximum of the beating portion to correspond with the requirements of frequency of the differential tone.

If these observations and deductions be correct, the contour of the graphic representation of a compound wave of two pure tones only affects the pitch of the tone at the change of direction and at the points where the wave forms pass the central position of the inner membrane of the ear. Having shown that an alteration of phase does not affect either the crossing points or the points of change in direction, this theory appears to be favoured by the remarkable experiments described by Helmholtz, proving the fact that alteration of phase practically makes no difference in the effect of the tone, although the contour of the wave may be considerably altered.

I will now direct your attention again to the phenomenon of the differential tones, with the view of showing the important part they play in determining consonance. It has been frequently stated that the differential tones are only heard when the primary tones are very loud, but I have always been able to detect them when the primaries are played with the greatest delicacy. Special attention is required to hear them, but they appear to be always there, and, to my ear, much more distinct than the harmonics. On the violin and other bowed instruments, also on the harmonium, they are especially noticeable from the continuity of the sound ; and even on the piano, the moment after striking the note, they can, with a little practice, be readily heard. Returning to Fig. 1, page 2, representing the effect of a constantly sounding note, with a sliding note gradually rising through the various musical intervals, we shall expect to find, according to what our diagrams have indicated, that the differential note between any two contiguous musical intervals, say the fourth and the fifth, should gradually rise through all the intermediate stages of vibration. Such is actually the case. If on a violin one of these intervals is sounded, say C and F, of 264 and 352 vibrations, or a note and its fourth, until we hear distinctly the differential 88 vibrations per second, and keeping the lower note, C, sounding, slide the finger on the upper note F, gradually up to G, the fifth, on listening carefully the differential note will be heard also rising as the upper finger rises, and when the interval is a true fifth, the differential tone has risen from 88 to 132 vibrations per second: in other words, while the principal interval is increasing a whole tone (from a fourth to a fifth) the corresponding differential tone has risen a musical fifth in its own position in the scale. A very slight deviation from a true fifth in the principal interval is therefore multiplied considerably in the corresponding interval of the differential tones. In gradually increasing the fifth, to a sixth, or modifying any other interval, the differential tone is heard to rise or fall according to the difference of the number of vibrations per second. I was first led to think about this from a method I had adopted instinctively, as an amateur violinist, in tuning my violin strings to perfect fifths. I concentrated my attention upon the differential tone which went wailing up and down, as the principal interval was adjusted, until the fifth was perfect, when the differential tone perched upon the exact octave below the lowest primary note, and as the variation on each side of this low note was a much larger proportion of its gamut than the contemporaneous variation in the higher notes to be tuned, it afforded a most perfect test of the truth of the main interval, any imperfection being multiplied considerably in the differential tone, and therefore easily heard. On reflection it will be seen that any other interval can be perfectly adjusted by adopting this means. This leads to the question whether this is not the unconscious method by which the ear recognises the accurate relationship between tones, the movement of the differential tone acting as a kind of natural differential gauge to determine the exact periodic coincidence of the waves of the higher primary notes, and at the same time adding to the combination the richness of its own effect. It is only when the differential tone is in harmonic relation with one or both of the primaries that the mind receives a pleasurable sensation, and the simpler this harmonic relation the more perfect will be the concord of the primaries. Since I commenced to judge of the truth of musical intervals by listening to the differential tones, I find my ear has grown much more sensitive to the slightest variation, and I am inclined to think that by directing the attention of young people to these tones, and training them to judge of the accuracy of intervals by this method, the ear would become a much more accurate instrument. At the interval of a major second to C in this octave, the differential tone is so low as only just to be a musical note of 33 vibrations per second, and as we cannot at that depth judge of the pitch of the tone, the utility of our gauge fails us, and consequently in this and the lower octaves the interval of a second is much more obscure than in the higher octaves, where the resultant note has a higher vibration number. Hence, I think we may account for the brilliancy of the small intervals in the high octaves of a piano, compared with the want of definition of the same intervals in the lower octaves. For the minor second, or semitone, we have little to guide us except memory and judgment, and the relationship which it bears to the higher note of the natural scale, the minor sixth, which is a perfect fifth above it.

In considering the effect produced by two pure tones sounding together, we recognise that there must be a relationship between the vibration numbers of the two notes, and this relationship is that their pulsations coincide at periodic intervals, and the fact that these pulsations do coincide is proclaimed to the ear by a differential tone, which also bears the same kind of relationship, viz., of periodic coincidence, to each of the primary tones.

And now, having considered the condition of harmony for pure simple tones, we must not forget that the tones of most instruments are compounded with a greater or less number of harmonics. These harmonics, especially the lower ones, affect harmony by creating beating notes. For instance, if a fifth is slightly out of tune, the second harmonic of the higher note and the third harmonic of the lower note will be very nearly but not quite the same note. Hence, they will produce a very faint beat. In order fully to show the effect of harmonics in determining harmony, I have constructed a diagram (Plate II.) of the effect of two notes rich in harmonics, one of them the note C^1 of 264 vibrations per second, set off to scale from a zero line 0 0 and supposed to sound at the same vibration rate continuously, while the upper note commencing at 264 vibrations passes up through all intervals to a twelfth from C^1 to G^1. Now we will suppose that the harmonics are heard up to the sixteenth, that is to say, up to a note of 16 × 264 = 4224 vibrations per second, which is several notes higher than the highest note on a piano, and is, practically, at the limit of musical definition. Then, following the same method of graphic representation, the second harmonic of the stationary sound will be represented by a horizontal line 2 2, parallel to the base, and at twice the altitude of the first line; the third harmonic by the line 3 3, three times the altitude of the first line, and so on to the sixteenth. We will now consider the sliding tone. The angle of the line representing this is arbitrary, but I have in this diagram fixed it for convenience at an inclination of one in three. The thick vertical ordinate passing through X will represent the position of the octave, and if we wish to represent the harmonics of this sloping line, it is evident that at the position of unison the harmonics will all coincide with the corresponding harmonics of the stationary tones, but at the octave they will be widely divergent, and the higher the harmonic the more nearly vertical will be the line drawn through the various points representing the harmonics. If we now lay down the vertical ordinates at the positions of aliquot intersection, as already described (page 2), we shall have a graphic representation of all the notes on the scale. If we continue these lines up, we shall find that they each cut through the exact intersection of certain horizontal and sloping lines, representing the harmonics; and the particular lines intersected thus, which are numbered at the margin, correspond in the ratio of their numbers exactly to the vibration ratio of the original prime tones. Thus, the vertical line representing the fifth cuts through the intersection of the second harmonic of the higher note and the third harmonic of the lower note; the ratio between the vibration numbers of the notes producing the interval of a fifth being as 2 : 3. So with the vertical line representing the position of a sixth (ratio of vibration 3 : 5). This line cuts through the intersection of the third harmonic of the higher note and fifth harmonic of the lower note. And the slightest deviation from the true interval of the prime notes will throw the harmonic out, and cause beating. Of course, the beating effect is very small indeed when we rise to the higher harmonics, but by this will be seen how the resultant tones, in determining intervals, are assisted by the harmonics in defining exactly the position of notes in consonance.

An examination of Plate II. will show that any interval, whether musical or non-musical, you choose to sound will produce a compound wave form which will be recurrent in its effect, though the recurrence may be so long in its period that the ear cannot recognise any relationship in the different periods. I have marked on the diagram circles where the harmonics coincide at the lowest position for each interval, and a little reflection will show that the remoteness of the recurrence of wave forms will be in proportion to the height of these circles above the base line. Thus, for a musical fifth, the second line representing the second harmonic of the higher note cuts the third harmonic line of the lower note exactly at the position of the fifth, or to put it in other language, the crest of the third of one system of waves coincides with the second of the other, and as the ear has to wait for a time corresponding to three wave-lengths before it recognises the relationship of the systems, we can depict the degree of consonance by the circle being placed three units of length above the base line. In the interval of the third (proportion 4 : 5), we have to wait for five complete waves to enter the ear before the relationship between the notes is clearly recognised. Hence, the circle representing the degree of harmony is placed on the fifth harmonic line, at which point you will notice that the fourth and fifth harmonic lines also cross. Generally, then, the vertical height of these circles above the base line strictly represents the degree of consonance possessed by any interval. According to this, the order of consonance in the ordinary musical intervals is as follows:—Unison, octave, fifth, perfect fourth, major sixth and major third, minor third, minor seventh and augmented fourth, minor sixth, major second, major seventh, minor second.

We have considered the effect of two notes sounding together, and the same reasoning should apply to the addition of a third note. This third note will have independent relations to each of the other two. There will be a greater number of harmonics and resultant notes in the compound tone, but if the chord be harmonious we shall find a strict relationship existing between not only the prime notes but the subordinate tones arising from them.

From the innate love of harmony arises the love of melody in which the notes are sounded in succession, the mind always referring each note to what is called the key-note of the piece, which may be compared with the stationary note in the diagram (Plate II.), supposed to be always sounding while the upper note is moving about. In melody the moving tone passes from one position to another, but in perfect intonation never deviates from the exact tonal positions fixed by nature.

The earliest melodies were of the simplest form, always in one key, and that generally the minor. As music progressed, changes of key-note were introduced, which, forming contrasts in the different phrases of the melody, gave an immense addition to the artistic capabilities of music. The harmonising of part music was another resource of the artist, and the cultivation of the ear progressing gave it increasing power to detect the more obscure relationships of the various tones of the scale. This we see vividly in comparing the crude music of the ancients with the exquisite melody and harmony of Mendelssohn, or the grand effects of Beethoven. And it appears that the recognition of the relationship of tones is still growing when we find the German school of Wagner, Brahms, etc., delighting in still more obscure tone relations and modulations.

The physical laws of harmony which we have been considering are only the very elements of the study of the beautiful in music; the flow of melody, the modulation of key, the resolution of discord into harmony, the variations in time, all give to the mind an artistic impression of motion, which, reflecting the activity of our own thoughts and feelings, affords us the highest degree of pleasure.

CHAPTER II

DESCRIPTION OF OHMOGRAPH AND AN EXAMINATION OF DIAGRAMS PRODUCED BY SAME. EVIDENCE OF RESULTANT-TONES. GENERAL CONSTRUCTION OF THE EAR.

Some years elapsed before I again took up this subject. The graphic method described in Chapter I. for illustrating the compound wave form was deficient in two respects.

First, the assumption that in a simple wave form the particles of air moved uniformly in velocity was, as Dr. Young pointed out, not strictly accurate, although for convenience he adopted that method.

Secondly, there was in the diagrams then given no indication of the effect of differences of amplitude.

Description of Ohmograph.—In order to make the compound diagrams accurate, the instrument shown on Plate III. was designed to produce and record curves of sines on a long sheet of paper, one simple wave form being produced at the upper edge of the sheet, another at the lower edge, and between them the compound wave form of the two simple tones. By this means the figures are easily comparable and conveniently available for study.

In the construction of this machine I adopted what is known in mechanics as a dog-crank, to avoid the errors due to obliquity of connecting rods. Two cranks of this kind, *a* and *b*, are placed one above the other; the top one, *a*, is driven by a rotating handle, *c*, and a rod a^1, in one piece with the dog-crank, from which it takes its to and fro motion, passes in front of a long cylinder, *d*, covered with indiarubber, revolving at right angles to the crank shaft, and driven from it by a pair of mitre wheels, *e e.*

The friction of the surface of this cylinder drives a second cylinder of brass, *f*, placed underneath and parallel to it. A rod, b^1, in one piece with the lower crank, also passes in front of the cylinder, taking its to and fro motion from the lower dog-crank.

The lower crank shaft gears with a toothed wheel, *g*, into another toothed wheel, *h*, on the upper crank shaft. These two wheels are cut with teeth, the numbers of which are of various ratios, and act as change wheels to obtain varying proportions of wave-length. A small wheel, *i*, covered with indiarubber to prevent slipping, rolls between the under side of the top connecting rod, a^1, and the upper side of a roller path, *j*, fixed on the frame; while a similar roller, *k*, rolls between the upper side of the lower connecting rod, b^1, and the under side of a roller path, *l*, also fixed to the frame. The pencils are fixed in the centre of these rollers, which in rolling move half the throw of the dog-crank. The points of these pencils, which are in a horizontal line parallel to the axis of the brass roller, press on a roll of paper which is drawn through between the upper and lower rollers.

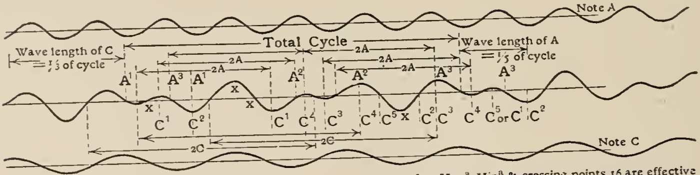
In order to produce the compound of the two simple harmonic wave forms a third roller, *m*, also with spring pencil and indiarubber tyre, is placed so as to roll between the two connecting rods, the result being that this centre roller, partaking of the to and fro motion of the two connecting rods, traces upon the paper, *n*, which is drawn between the two cylinders from the spool, *o*, a curve, the vertical ordinates of which represent the algebraic sum of the corresponding ordinates of the simple wave forms.

To get varying amplitude, the crank pin is, in each dog-crank, made movable, so that it can be fixed nearer or farther from the centre of the crank shaft. To alter the phase one of the driving wheels must be disengaged and one crank moved round to any angular position relative to the other crank that may be desired.

With this machine many diagrams have been made of various harmonious and dissonant intervals, not only of equal but of varying amplitude, also with phases starting in various relative positions.

Fig. 3 shows one of these compound wave forms, the original components, C and A, being in the vibration ratio of 3 : 5 of equal amplitudes and similar phase.

This interval is a musical major sixth, as indicated by the letters C and A (musical notation). If we examine this diagram, we shall find that in the original wave forms C and A the periodic impulses are indicated by the equal distances from the crest to crest and from hollow to hollow of each simple wave form. In the compound wave form there are still crests and hollows, but they do not exhibit the frequency of either of the original tones which we can distinctly hear when the two notes are sounded, as though we were endowed with a special organ for each simple sound.



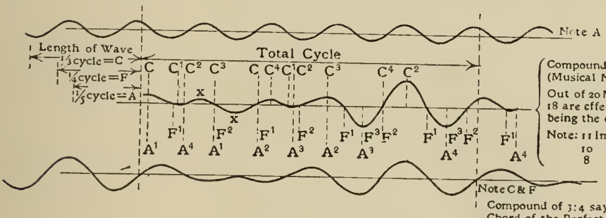
Out of 20 Max.^{a}, Min.^{a} & crossing points 16 are effective
Those 4 marked x being the only non-periodic impulses.

FIG. 3.

As we know by the evidence of our sense of hearing that both tones do reach the brain, there must be between the tympanum and the brain some process by which the frequencies of both notes are restored.

If we turn again to Fig. 3 and with a pair of compasses measure the distance from crest to crest of the simple wave form C, then apply the compasses to the compound diagram of C and A, it will be found that although from the consecutive crests and hollows we do not discover the period of C, yet, if we regard each point where the curve crosses the axis as being an impulse point, there are several periodic impulses in each complete cycle of change.

If the points of the compasses be applied to the lower wave form of the note C, we find C^1 C^1 — C^2 C^2 C^2 — C^3 C^3 — C^4 C^4 — C^5 C^5 in the compound, all of which are in five different groups periodic, and correspond to the period of the original note C; also A^1 A^1 — A^2 A^2 — A^3 A^3, all periodic, and corresponding in three different groups to the original note A. We also find a number of recurrent impulses, 2C and 2A, which represent the octave below C and A and would therefore assist the harmony. If we include these, we have out of 20 maxima, minima, and crossing points in the whole cycle 16 effective, those four marked x being the only non-periodic impulses.


Note A
Length of Wave
1/3 cycle=C
1/4 cycle=F
1/5 cycle=A
Total Cycle
C C¹ C² C³ C C⁴ C¹ C² C³ C⁴ C²
x
x
F¹ F² F¹ F² F¹ F³ F² F¹ F³ F² F¹
A¹ A⁴ A¹ A² A³ A² A³ A⁴ A⁴
Note C & F

Compound of 3:4:5 say C.F. & A (Musical Notation) Chord of the $\frac{6}{4}$
Out of 20 Max.ᵃ, Min.ᵃ & crossing points 18 are effective. Those marked x & x being the only non-periodic impulses.
Note: 11 Impulses effective for Note C
10 " " " " F
8 " " " " A

Compound of 3:4 say C & F (Musical Notation) Chord of the Perfect Fourth.

FIG. 4.

This test of the theory becomes much more stringent if we add the ratio of 4 in the same cycle, making a triple compound 3 : 4 : 5. Fig. 4, shows this combination, which is known by musicians as the chord of the $\frac{6}{4}$. The lowest note is C, the next above F, and the top note A, according to musical notation.

Adjusting the compasses to the wave-length C, it will be observed that C C — C^1 C^1 — C^2 C^2 C^2 — C^3 C^3 — C^4 C^4 are each periodic, though in five different groups; also F^1 F^1 F^1 F^1 — F^2 F^2 F^2 F^2 — F^3 F^3, periodic in three groups; also A^1 A^1 — A^2 A^2 — A^3 A^3 — A^4 A^4, all periodic in four groups. In the whole cycle there are 20 maxima, minima, and crossing points, of which 18 are effective impulses coincident with the original components—those two marked "xx" being the only non-periodic impulses, and which would therefore go to produce noise.

The term "effective impulses" as applied here means that out of 20 total impulse points 18 of them are periodic, and therefore effective, and, although in different groups, produce, as I shall presently show, upon the sense of hearing the impulses of the three original simple tones.

On Fig. 5, I have plotted down the compound of

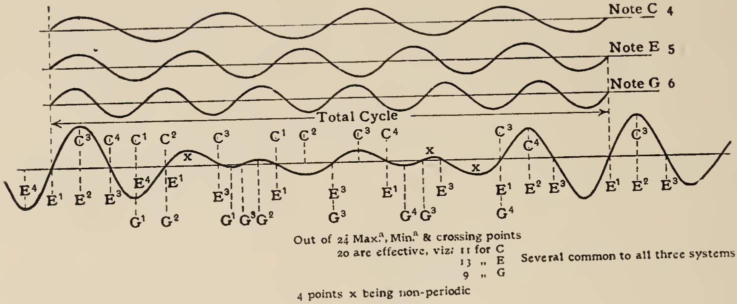
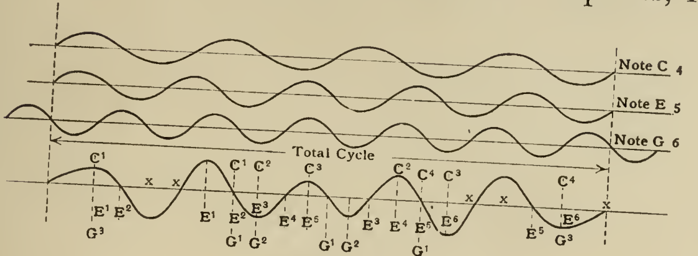

Note C 4
Note E 5
Note G 6
Total Cycle
C³ C⁴ C¹ C² C³ C¹ C² C³ C⁴ C³ C⁴ C³
x x x x
E⁴ E¹ E² E³ E⁴ E¹ E³ E¹ E³ E¹ E³ E¹ E² E³ E¹ E² E³
G¹ G² G¹ G³ G² G³ G⁴ G³ G⁴
Out of 24 Max.ª, Min.ª & crossing points
20 are effective, viz: 11 for C
13 " E
9 " G
Several common to all three systems
4 points x being non-periodic

Fig. 5.

notes forming the well-known musical chord of the $\frac{5}{3}$, or major triad C, E, G. The ohmograph, as at present constructed, is not available for producing a combination of more than two tones, but the plotting of the curve is quite simple, and to such a scale as that shown is really more accurate than by any other graphic method, though somewhat tedious to produce. It will be seen that in this case out of 24 maxima, minima, and crossing points 20 are effective, viz., 11 for C, 13 for E, and 9 for G (several being common to all systems), while four impulses x are non-periodic.

In Fig. 6, the combination is the same, except that the highest note, G, is placed half a wave-length in advance of the C and E.

The difference in the compound is very marked in contour, but it will be seen how curiously the sinuosities of the curve adapt themselves to the requirements of periodic impulses. We find that out of 20 maxima, minima, and crossing points we have 8 C impulses, 13 E impulses, and 7 G impulses in the whole cycle, or out of 20 impulse points 15 are effective and many common to all systems.



Out of 20 Max.ª, Min.ª & crossing points
15 are effective, viz: 8 for C
13 „ E
7 „ G
Several common to all three systems
5 points x being non-periodic

FIG. 6.

If we now add another note to the above and compound four ratios, viz., 4 : 5 : 6 : 7, forming the chord of the minor seventh, C, E, G, B♭, we find the wave form as shown in Fig. 7. In this case it will be seen that although

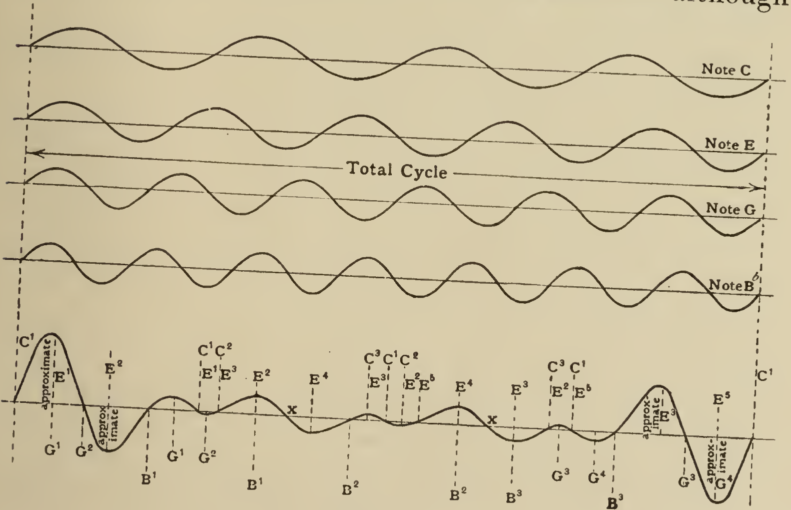


FIG. 7.

the sinuosities of the compound curve are greatly altered from those in Figs. 6 and 7, yet they adjust themselves so as to make the impulse points periodic for each of the four systems, and we find that in this case, out of 28 maxima, minima, and crossing points, 26 are effective, viz., 8 for C, 15 for E, 8 for G, and 6 for B♭, many being common to all the systems.

Musicians generally resolve this so-called dissonant chord into that of the $\frac{6}{4}$. In this resolution the dissonant B♭ descends to A, and E ascends to F, while G descends and merges in F.

Perhaps this is the right time to state that it is not claimed that these spaces in the compound figure representing period are absolutely and mathematically accurate. I have placed some of these diagrams before two well-known mathematicians, and they have worked out some of the relative positions of the crests, hollows, and crossing points. They inform me that, although not all mathematically accurate, yet they may be sufficiently so for the theory, as the ear, in judging of musical intervals, does not depend upon absolute accuracy of vibration ratio, a fact well known to practical musicians. Later it will be shown that owing to the elastic resistances of the ossicular muscles and the sub-arcuate zone of the basilar membrane a change takes place in the pressure wave form of the liquid which makes the time positions of the impulse points much more accurately periodic.

As every one of these compound diagrams will vary according to change in amplitude of each original tone, also in the relative phase of the varying waves, the calculations involved to determine the periods of these vibrations in any one case would be endless. I therefore content myself by adding at the end of this chapter an addendum to the paper published in 1907 giving particulars taken by my instrument of all the chief musical and some dissonant intervals, with many variations of amplitude and phase, which will show that in each case cited the same law appears to hold good.[1]

It should be noted that if these curves be regarded as compression and rarefaction curves, each crossing point corresponds with the moment when the membrane of the fenestra ovalis is in its normal central position (this is demonstrated later; see p. 76).

Before the results in the appendix are examined it will be well to consider what are the conditions under which a succession of impulses produces on the ear the sensation of continuous sound.

It does not appear to be necessary in order to hear a note sounding continuously that the impulses should be continuously periodic. If a Seebeck's syren (Fig. 8, p. 32) be drilled in a complete circle with equidistant holes and a blast of air be directed against this circle when the syren is revolving, several of these holes may be closed at different parts of the circle, and we still hear the proper tone with intervals of silence, if the closed holes do not extend over too large a proportion of the whole circumference.

Again, if holes, say four, be drilled equidistant, then a short space of different dimensions, say one-seventh of the longer space, followed by another group of four equidistant holes, then another short space, differing from the first, two-sevenths of the longer space, and so on all round, increasing the short space each change by intervals of one-seventh of the long space so as to ensure an inharmonic break between each group. When this circle of holes is blown upon, the note due to the equidistant groups of holes is distinctly heard, but with a less musical effect.

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[1] The very numerous diagrams mentioned as in an appendix have not been reproduced in this volume, but they can be supplied to anyone who may be interested in following up the investigation. They are to a much larger scale than those in this publication and are all included in my paper published in 1907 (by Kell & Co., Covent Garden) in a separate binding. At the end of this chapter I have reproduced a table which gives the result of each diagram taken in the 1907 publication.

If, instead of four equidistant holes in a group, three should be drilled, followed by a short space, a still less musical effect is produced. If two holes are drilled in a group, followed by the break of a short space, and so on all round, very little musical effect is heard, but an abundance of noise.

In the syren (Fig. 8) there are in the outside circle

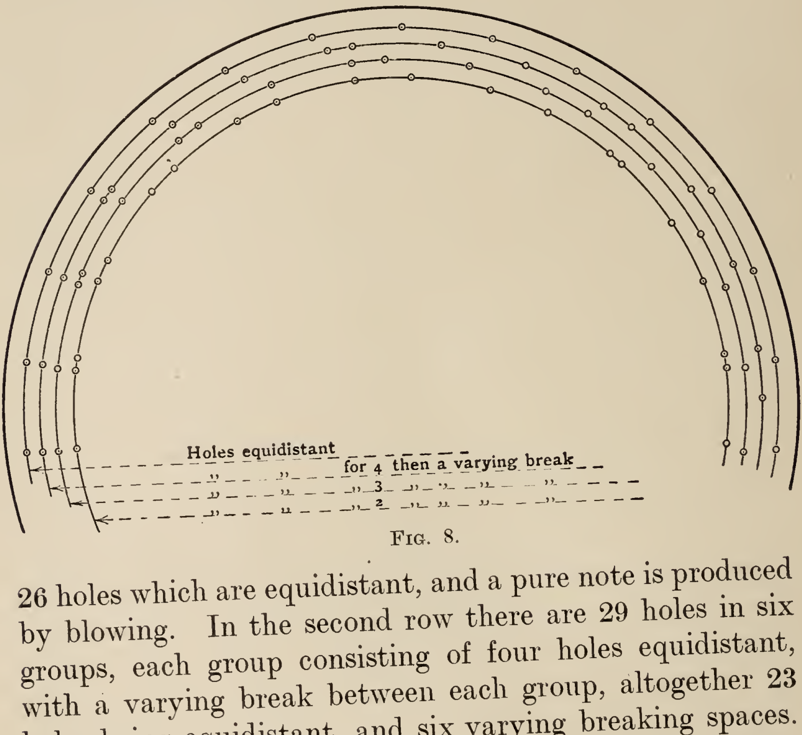


FIG. 8.

26 holes which are equidistant, and a pure note is produced by blowing. In the second row there are 29 holes in six groups, each group consisting of four holes equidistant, with a varying break between each group, altogether 23 holes being equidistant, and six varying breaking spaces. In this the note is clearly heard, but mingles with a certain amount of noise.

In the third row there are 31 holes in 10 groups, each consisting of three holes equidistant, with a varying break between each group, altogether 21 holes being equidistant, and 10 breaking spaces. In this the note is heard, but still less clearly—the noise being greater. In the fourth row there are 32 holes in 16 systems, each consisting of two holes equidistant, with a varying break between each system, altogether 32 holes and 16 breaking spaces. In this the note can scarcely be recognised, being nearly drowned by the noise produced by the non-periodic impulses.

In the first row	100 per cent. of the holes are equidistant			
In the second row $\frac{23}{29}$ or ..	80	,,	,,	,,
In the third row $\frac{21}{31}$ or ..	68	,,	,,	,,
In the fourth row $\frac{16}{32}$ or ..	50	,,	,,	,,

Since making the above experiment, I have come across a paper read before the Royal Society, November 26th, 1891, by Herroun and Yeo, upon the audibility of single sound waves, and the number of vibrations necessary to produce a tone.

From their most interesting experiments the authors came to the important conclusion that where sound is produced by a vibrating body, each individual wave of the syren causing the tone stimulates the terminals of the auditory nerve. Also that the immediate succession of two waves gives rise to a sensation of tone having the same pitch as that yielded by a prolonged series at the same rate. That is to say, we can distinguish the tone produced when only two vibrations of a series reach the terminals of the auditory nerve.

This proves that two periodic impulses in each cycle of a compound diagram are sufficient to appeal to the ear as a tone, though in my diagrams there are more in each cycle.

In addition to the impulses indicating the original tones, other periodic impulses appear in the compound air figures when we regard the crossing points as producing impulses.

Differential Tones are well-known and easily heard tones which have a vibration rate equal to the difference of those of the primaries. In the case of tones having vibration ratios with a difference equal to unity such as 2 : 3 — 3 : 4 — 4 : 5 — 5 : 6 — 8 : 9, it is clear that once in every complete cycle there will be an exact recurrence of *every* point of the compounded wave form in the previous cycle. This single recurrence of every impulse in each cycle corresponds with the differential tones, 3 minus 2, 4 minus 3, 5 minus 4, etc. When there is a difference of two or three in the ratios, as in the case of 3 : 5 — 5 : 7 — 5 : 8 or 4 : 7, the differential is indicated by two or three equidistant recurrences in each cycle, corresponding with the required frequency of the differential tone.

Summational Tones are faint tones above the two primaries which have a vibration rate equal to the addition of those of the two primaries. Examination of the diagrams will show that in almost all cases there are indications of the summational tones in the compound air diagram if the crossing points are regarded as points of impulse. Where the amplitudes are the same or very nearly the same, and especially where the difference of the lowest numbers representing ratio of frequency is equal to unity, the crossing points appear to coincide with the summational tone; but variations from these conditions appear to render their identification more obscure. I have marked, in a number of diagrams, the points " S " which give impulses corresponding to the summational tone. It is not necessary, according to the hypothesis, to suppose that it is only the crossing points that furnish the impulses for the summational tones; the crests and hollows may also be considered effective, and the points of impulse may form several groups or systems within each cycle, as in the case of the principal impulses.

From an examination of the numerous diagrams of compound notes given in the appendix the general conclusions are :

First, that in most cases equal amplitude and the starting at similar phase will give the most perfect realisation of the hypothesis.

Secondly, that a deviation from either of these conditions introduces impulses which are non-periodic, and therefore contribute to noise, but not to such an extent as to prevent the larger percentage of impulses being periodic in several systems or groups, and therefore producing the sensation of harmony.

For instance, if we again turn to the diagram (Fig. 3, p. 26) representing a musical major sixth (musical notation C A), we find that out of 20 maxima, minima, and crossing points we have 16 which are periodic with either one system or the other, and the remaining four, marked "x" (20 per cent. of total impulses), are inharmonic to either system. The diagrams also show that variation in amplitude or phase may vary the proportion of harmonious to inharmonious impulses so as to make the same intervals more or less perfect. (See end of this chapter for table of percentages of harmonious impulses taken from my paper published 1907.)

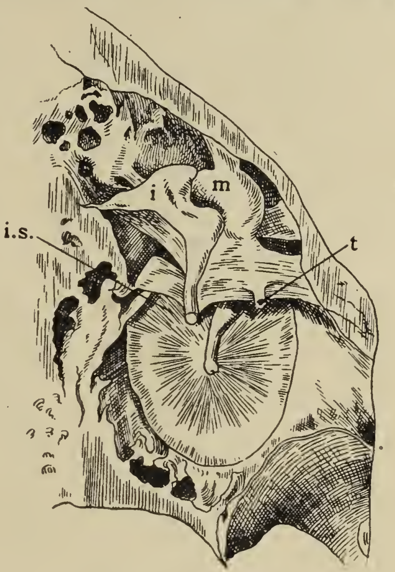
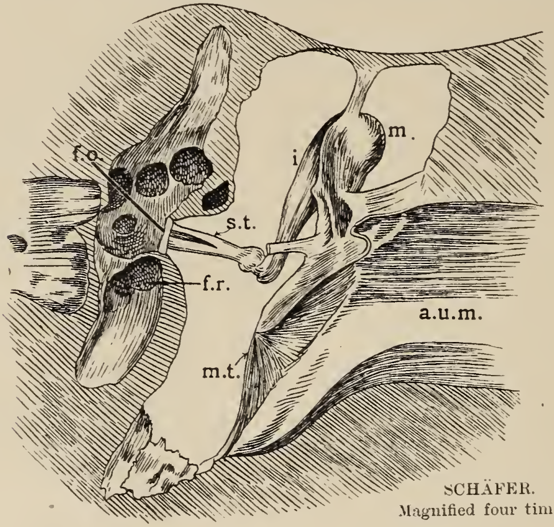


Fig. 9.—Tympanum Laid Open Exposing the Membrana Tympani on its Outer Wall.

t. Attachment of tensor tympani to handle of malleus.
m. Head of malleus.
i. Short process of incus.
i.s. Posterior-superior area of membrana tympani. (After Guibé.)

General Construction of the Tympanum, Tympanic Ossicles, and Cochlea.—The ear is the organ that receives the pulsations of air which, in the form of successive condensations and rarefactions, arrive at the drum of the ear, a membrane vibrating in a frame nearly circular (vertical diameter, 10 mm. ; horizontal diameter, 8·5 mm., Sappey). Figs. 9, 10, 11, show the general features of the arrangement of parts. The membrane of the tympanum is highly elastic, so that it responds readily to the varying pressures of the air waves as they enter the auditory meatus.

The to and fro motion is transmitted to the fenestra ovalis (which separates the middle ear from the labyrinthine liquid) by three articulated bony levers (Fig. 12). The malleus *m.* is articulated with the incus *i.* in such a way that they rotate together through a small angle. As the point of the malleus is fastened to the umbilicus of the drum membrane, the movement of the latter is conveyed through the articulated joint between the malleus and the incus into the stapes which is hung in the fenestra ovalis, the membrane enclosing the liquid

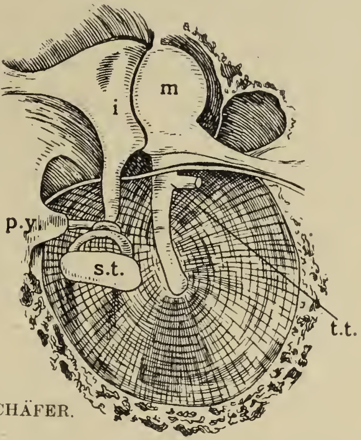


SCHÄFER.
Magnified four times.

FIG. 10.—VERTICAL SECTION ACROSS THE TYMPANIC CAVITY (AFTER SCHÄFER).

a.u.m.	External auditory meatus.
m.t.	Membrana tympani.
m.	Head of malleus.
i.	Body of incus.
s.t.	Stapes.
f.o.	Fenestra ovalis.
f.r.	Fenestra rotunda.

in the cochlea. On Fig. 11, will be seen at *t.t.* the position of a slender muscle known as the tensor tympani. The tendency of this muscle is to draw the drum and the stapes inwards. The antagonistic muscle to this is the stapedius, which tends to lever the footplate of the stapes outwards. This muscle takes hold of the top of the stirrup of the stapes; see Fig. 13, where *p.e.* the posterior end of the fenestra ovalis, is shown to form a kind of ligamentous hinge with the foot of the stapes. The contraction of the stapedius muscle, *s.m.*, acting on the head of the stapes concurrently with the expansion of the tensor tympani balances the ossicles of the tympanum and regulates the degree to which the liquid within the cochlea is



SCHÄFER.

Fig. 11.—The Relationship of the Ossicles to each other and to the inner Aspect of the Membrana Tympani (after Schäfer).

m.	Head of malleus.
i.	Body of incus.
p.y.	Pyramid.
s.t.	Stapes.
t.t.	Tensor tympani.

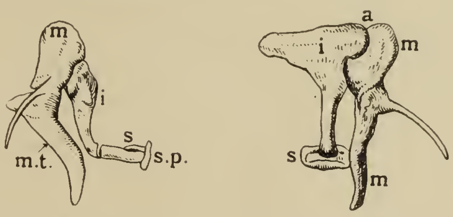


Fig. 12.—Two Views of the Articulated Ossicles.

The first shows those of the right side viewed from the front of the ear; the second the same set viewed from the outer side.

m.	Head of malleus.
m.t.	Aspect of handle applied to membrana tympani,
i.	Incus.
s.	Stapes.
s.p.	Foot-plate of stapes,

displaced. Fig. 14 is a transverse section of the stapes showing the membranes of the *f.o.* attached. The top of the malleus is suspended from the roof of the middle ear (see Fig. 10) by a ligament, *m*, and is also supported tightly by ligaments crossing in front and behind the malleus, forming a ligamentous hinge marked *h* (see Fig. 15). The articulations being above this ligamentous axis, the stapes at the end of the long arm of the incus moves in the same direction as the tympanic membrane. We thus have the tympanic membrane and its ossicles hung in elastic bands ; two of these, the tensor tympani

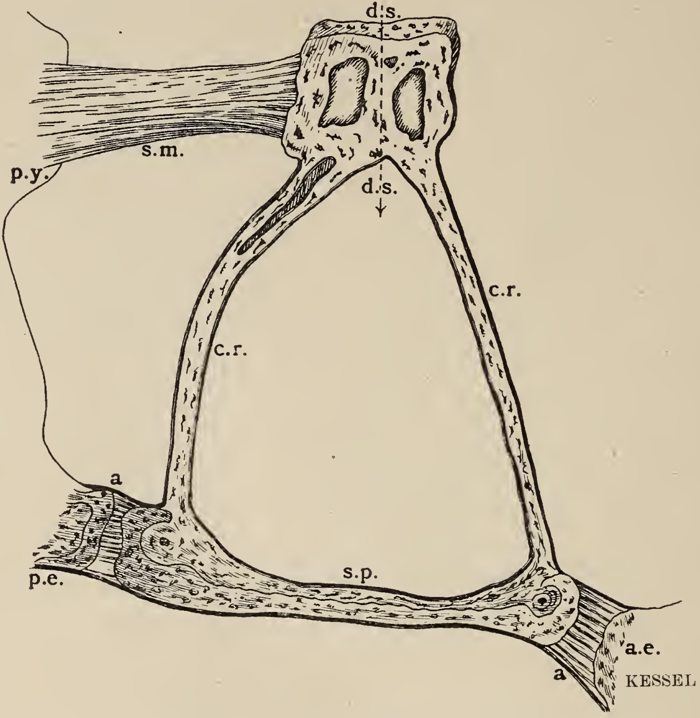


Fig. 13.—Diagrammatic Section (Kessel) of the Stapes, made in situ. The Foot-plate is fixed in the margins of the Fenestra Ovalis by Fibres of the Annular Ligament a.a.

p.y. Pyramid.
s.m. Tendon of stapedius muscle.
p.e. Posterior end of fenestra ovalis.
a.e. Anterior end of fenestra ovalis.

and the stapedius, oppose each other, being attached to the fixed walls of the middle ear.

Mechanism of Middle Ear.—This method of hanging, moving membranes in which opposing elastic forces tend to resist motion to right or left appears to derive its efficiency from the fact that when the membrane moves to the right the elasticity helping it in that direction is balanced in the case of small vibration by the elasticity in the opposite direction. If a piece of indiarubber be *well* stretched to obtain an initial tension between two points *B* and *C* on a board (Fig. 16), take hold of this rubber at the centre *A* and pull it to the right; all the initially stretched elastic particles to the left of *A* are opposing this motion, but the particles to the right are assisting; the result is that the forces in the elastic balance each other at the centre, and practically the whole of the moving power applied at *A* is transferred to the medium to be put in motion for a small range. This gives great sensitiveness to the transmission of power in small vibrations. The principle in its application to the middle ear is the same as illustrated in Fig. 16, although to get the ligaments supported in the fixed walls of the middle ear they must pull upon bent levers as shown in schematic section, Fig. 17.

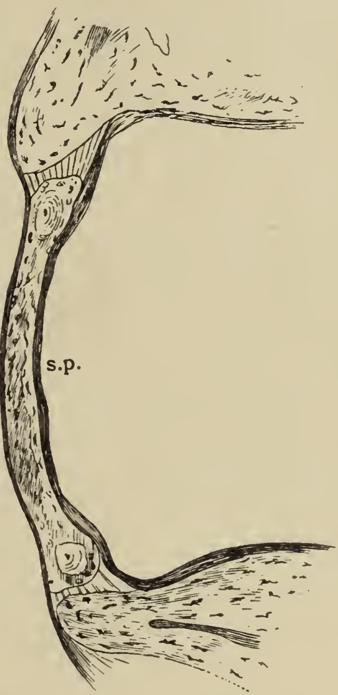


Fig. 14.—Section of the Foot-plate of Stapes and Fenestra Ovalis at Right Angles to the one shown in Fig 13.

In fact, the ossicles and the antagonistic muscles form a kind of balance wheel, with an action not altogether dissimilar to the balance wheel of a watch, only the range in the watch balance wheel is uniform in its amplitude of

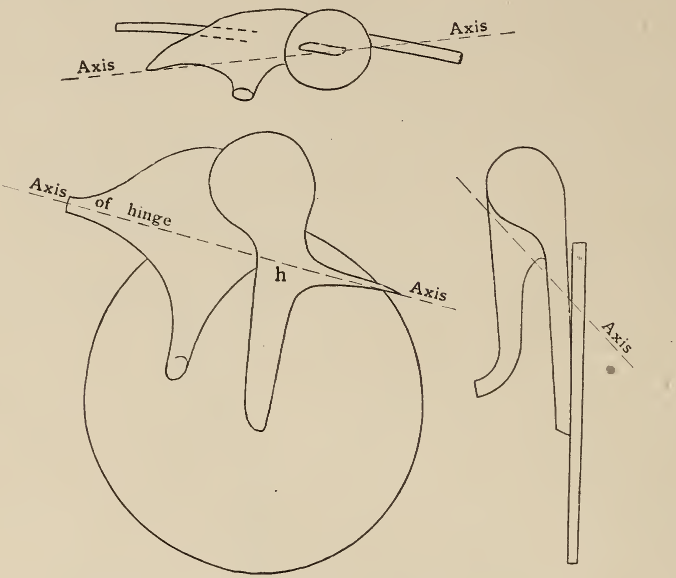


Fig. 15.—Schematic Sketch of Ossicles.

vibration through the action of the main spring and escapement, whereas in the ear the range varies according to the varying pressures and displacements of the sound wave which causes its motion.

There are on the surfaces of the articulation between the malleus and incus, toothlike processes fitting

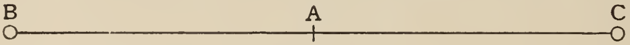


Fig. 16.

into each other, enabling each to drive the other in the to and fro movement of the membrane, but in case of unusually sudden sound disturbance, these will slip over each other, and so prevent undue shocks which might cause rupture of the membrane, if transmitted too suddenly to the liquid of the cochlea.

By this continuous connection between the drum and the footplate of the stapes in the fenestra ovalis we have the means of getting a positive *push* transferred to the stapes alternating with a positive *pull* as the condensations and rarefactions of the air waves respectively arrive at the drum. The movement back of the drum membrane is caused by the atmospheric pressure which exists in the middle ear, pressing on the interior surface of the drum membrane as the wave form pressure diminishes at the exterior surface. This atmospheric pressure acts on the fenestra rotunda at the other end of the cochlea, which also opens into the middle ear. The liquid thus moves to and fro in the cochlea, following the condensations and rarefactions at each part of the wave form.

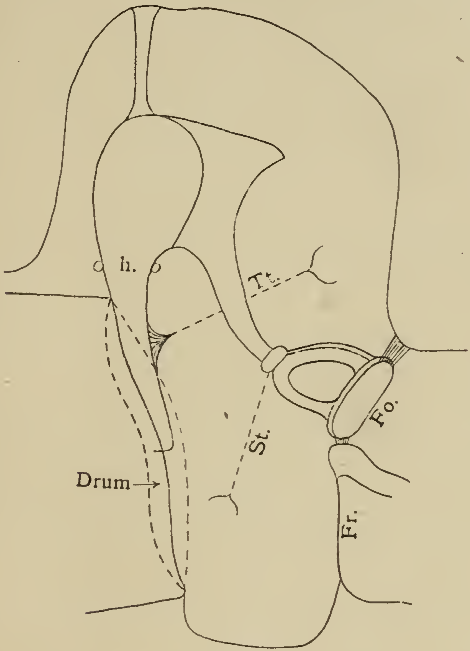


Fig. 17.—Diagrammatic Vertical Section across Tympanic Cavity, to show lines of Traction of Tensor Tympani (Tt.) and Stapedius (St.).

The initial tension in the two muscles pulling on the ossicles will always cause the membranes to come into the central or normal position, because, referring to Fig. 16, the position *A* can only be stationary when the tension on the right of *A* is equal to that on the left.

It will be presently shown that the basilar membrane also has an initial tension upon it which tends to bring it always back to the central position at the same moment as the stapes and drum membrane through the opposing action of the tensor tympani and stapedius muscles have been brought to their central positions.

Motion of Stapes.—Helmholtz in his "Tonempfindungen" (Ellis's translation) describes the to and fro motion as follows :—

" The excursions of the foot of the stirrup (stapes) are always very small, and according to my measurements never exceed 0·1 of a millimetre."

He also states that " the foot of the stapes is fastened into the membrane of the oval window and fills it up with the exception of a narrow edging." Also that in its action " the upper and somewhat looser edge of its foot is more displaced than the under."

Annular Membrane.—Since the time of Helmholtz there has been much examination of the stapes, and it has been shown that the membrane is of varying breadth all round the fenestra ovalis, and that the part of the stapes where the membrane has least breadth forms a species of hinge, somewhat similar to the hinge of a bucket in an ordinary lift pump. Moving on this as a centre, the to and fro motion of each part of the foot of the stapes varies according to its distance from the axis of motion.

The Stapes.—Fig. 13 shows a magnified section, according to Kessel,[1] through the long axis of the stapedial footplate, and Fig. 14 the cross section. It will be seen that the stapedius muscle, which passes from the head of the stapes to the pyramid, *py.* (see also Fig. 11), exercises its pull in a direction parallel to the long axis of the fenestra ovalis, so that it tends to revolve the stapes round the hinge at its posterior end, thus drawing the anterior end of the stapes outwards.

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[1] See Schwartze's " Handbuch der Ohrenheilkunden," 1892, pp. 92–93.

Fig. 13 shows very clearly the way in which the stapedius muscle rising from the pyramid, *py.*, tends to cause this hinge motion.[1]

This muscle is balanced by the tensor tympani, which is attached to the malleus at a point just under the ligamentous axis, on which, with the incus, it turns (see Fig. 11).

These two muscles are therefore antagonistic, and tend to keep the membrane of the fenestra ovalis in its central position when there is no wave passing.[2]

The foot of the stapes (Fig. 13) is closer to the posterior than to the anterior end of the fenestra ovalis. The difference is considerable, the breadth of the ligament being, according to Guibe,[3] also according to Eysell,[4] 0·015 mm. at the posterior and 0·1 mm. at the anterior end, a difference of breadth of nearly six and a half to one.

The mean direction of pressure from the incus passes through a point between the centre of the long axis of the stapedial plate and the anterior end (see note on Dr. Keith's drawing, Fig. 17A ; also see Fig. 13) through the stirrup-shaped crura of that ossicle, and the stapedial plate rocks through a small angle to and fro on the hinge.

For further evidence on this point, Politzer states that

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[1] From "Diseases of the Ear," by Politzer, translated by Ballin and Heller, 1902, pp. 9, 34.

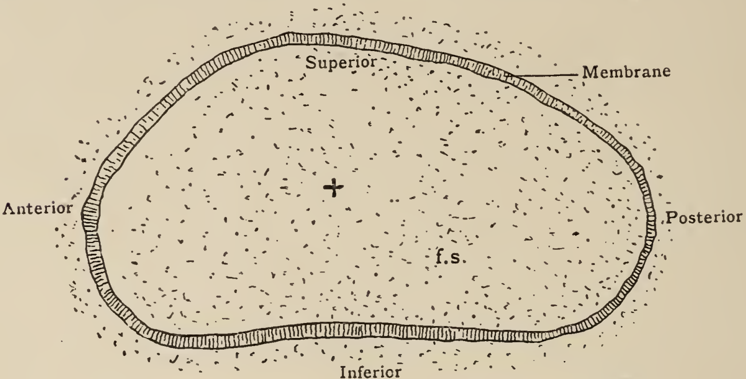
[2] Kleinschmidt, in a paper on Sound Conduction through an Air Chamber, found that a plate or membrane must be in perfect equilibrium to respond to the slightest air movements. "Recent Theories of Sound Conduction," by Dr. Treitel, Berlin.

[3] See Poirier's "Anatomy," p. 1308.

[4] See Schwartze's "Ohrenheilkunden," 1892, p. 89.

Mach and Kessel found by optical examination of the motion of the stapes that it "did not perform a piston-like motion in the fenestra ovalis, but that it turns on an axis situated near the inferior margin of its footplate that causes the superior margin of the footplate to penetrate deeper towards the vestibule than the inferior." [1]

Notwithstanding the hinge motion of the stapes, which would in its application to the liquid cause inequalities in the forward motion of the liquid close to the front of the stapes, the actual power transmitted would be in proportion to the displacement multiplied by the pressure. This will be dealt with later.



f.s. Footplate of Stapes

+ Marks the approximate position of the point through which the pressure from the top of the Incus passes through the foot plate.

Fig. 17a.—Section to Expose the Annular Membrane which Binds the Foot-plate of the Stapes within the Margin of the Fenestra Ovalis. Made from a Microscopic Section parallel to the Foot-plate (Keith).

If we again look at Kessel's illustration, Fig. 13, showing the hanging of the stapes in the fenestra ovalis, we observe that the pull of the stapedius muscle is upon a bent lever formed of the stapes itself, the fulcrum of which is at the posterior end of the fenestra. At the anterior end the drawing shows a series of strong ligaments forming what is known as the membrane of the fenestra ovalis.

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[1] See Politzer in "Diseases of the Ear," translated by Ballin and Heller, 1892, p. 58.

Fig. 18 shows a section made by Dr. Keith of this membrane on each side of the shorter axis of the stapes. The measurements taken by Dr. Keith show that the thickness of the membrane is, on the upper side, 0·3 mm. According to Helmholtz the longest excursion of the stapes is 0·1 mm.; if this refers to the centre of the stapes the motion is only one-third of the thickness of the membrane.[1]

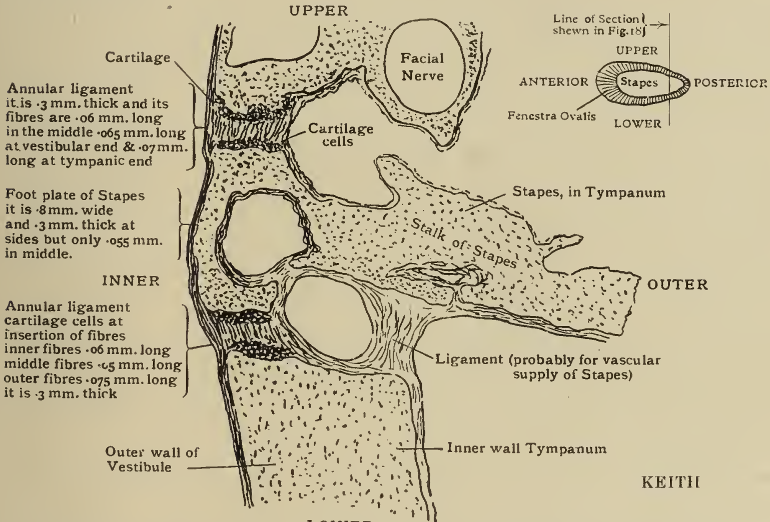

Fig. 18.—Vertical Section of Foot-plate of Stapes showing the Structure of the Annular Ligaments which bind it to the Margin of the Fenestra Ovalis (Keith).

If we admit that the function of the tensor tympani and stapedius muscles is to maintain the balance of pressure between the inner and outer ear, we shall see that this is most simply done if a hinge exists.

Dr. Keith informs me that the malleus and incus are not essential for hearing, as

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[1] It is probable that the fibres connecting the stapes with the frame of the *f.o.* may be partly elastic and partly inelastic, so that the latter would resist definitely any extreme pressure on the stapes, and the former would act as an elastic resistance up to the limiting position of the inelastic fibres.

(1) Their removal still allows the perception of sound, which, though less acute, is unaltered in quality and character.

(2) In amphibia, in reptiles, and in birds, the stapes, the incus, and the malleus are represented by a single bone —the columella—a stethoscope-like bone attached at its flat end to the tympanic membrane ; at its other end it swings in the fenestra ovalis with a rocking motion, and there are no other ossicles.

Dr. Keith points out that if the auditory human ossicles have to do with the regulation of the pressure of the perilymph and endolymph, the arrangement of the muscles in connection with the chain of bones becomes clear. See Fig. 17, which is a schematic section through the middle ear.

In the first place, two elastic muscles under initial tension are continually acting in opposite directions on the chain of ossicles to balance them. When the tensor tympani contracts it has the effect of plunging the stapes deeper in its fenestra and increasing the pressure of the fluids in the inner ear ; the stapedius has exactly the opposite effect, and through the balance maintained by these muscles the pressure of the liquids in the inner ear is regulated.

The stapedius is so placed as to be incapable of exercising a piston-like action on the stapes as assumed by Helmholtz and other writers, but it is admirably arranged to act on the stapes as a bent and hinged lever to pull the anterior end of the stapes outwards. If the antagonistic action of these two muscles be admitted, it appears to require the existence of a hinge to render it effective. There is no necessity to assume a piston-like movement, as if the upper part of the foot of the stapes moves further in than the lower or hinged part, the pressure in the liquid which fills the cochlea transmits its pressure in every direction immediately according to the law of liquids in a closed vessel.

On Plate IV. is a drawing made by Dr. Keith, ten times life size, showing a view from the tympanic side of the drum membrane, also a horizontal and vertical section showing the attachment of the malleus to the umbilicus of the membrane. It was observed by Helmholtz that although the general form was concave there was a slight convexity on the outer side near the periphery of the membrane. In Dr. Keith's section this is clearly shown. If the membrane were of purely conical section, pressure on the membrane outside would move the handle of the malleus forward against a tensile strain passing radially through to the implantation ring and would cause a restraining action on the movement of the malleus. This strain is got rid of by this convexity outwards as the pressure over the whole surface of the membrane tends to straighten out this convexity without putting radial tensile strain upon the ring, and practically the whole of the units of pressure would pass into the handle of the malleus. This device is frequently used in the case of hydrostatic pistons where great sensibility is required in the transmission of pressure through the membrane and where radial tension would destroy this sensitiveness.

Helmholtz recognised the necessity of the pressure in the cochlea being largely reinforced, but he omits to notice that the chief cause of this reinforcement is undoubtedly the great difference in area between the drum membrane and the effective area at the fenestra ovalis.

A very usual mechanical method in hydraulics of increasing the unit pressure in a liquid (Fig. 19) is to admit the lower pressure to the bottom of a ram working in a cylinder of large area and to reduce the ram above the gland of the cylinder so that it passes into another cylinder of smaller area through another gland.

If the effective unit pressure in the larger cylinder is P, then area × P = total pressure upwards. This is concentrated upon the smaller area above, and therefore the unit pressure in the upper cylinder is increased.

The total pressure on each area will be the same, but the unit pressure in the two cylinders will be (disregarding friction) in inverse proportion to the areas, and it is clear that as the rams move together and have the same stroke the pressure will be in the inverse proportion to their displacement.

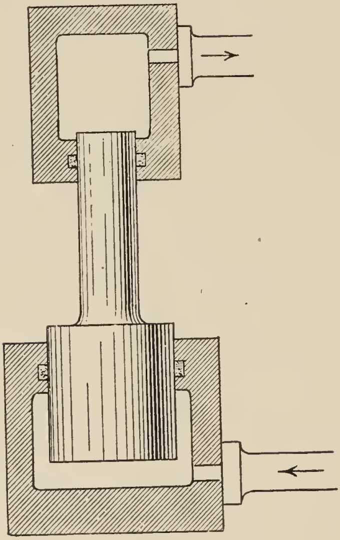

Fig. 19.

I remember when a pupil at the Elswick Works long before Helmholtz wrote his "Tonempfindungen" that the form of Bramah press used by the late Lord Armstrong for testing hydraulic pipes was based on this principle. The low pressure had an effective head equal to about 400 lb. per sq. inch, which was admitted into a lower cylinder of 392 sq. inches area so as to give a total moving force of, say, 157,000 lb. This, when concentrated in the smaller area of the top cylinder, which was one-fifth the area of the lower one, raised the unit pressure in that cylinder to about 2,000 lb. per sq. inch, which was sufficient for testing purposes.

The measure of the increase in unit pressure was the lessening of the displacement to one-fifth, and thus multiplying the unit pressure in the upper cylinder by 5 = 2,000.

Now if, instead of making the lower ram to move in one piece with the upper ram, certain levers were introduced so as further to reduce the stroke of the upper ram without interfering with that of the lower ram, these levers will augment the total pressure and diminish the stroke, and therefore the displacement of liquid in the upper ram.

The effect of the increase of pressure due to the different areas remains, but is augmented by the intermediate leverages, and the effective pressure is increased in inverse proportion to the displacements. This is analogous to the action of the pressure of the air waves upon the large area of the drum membrane, which is fifteen to twenty times that of the stapes.

It will reduce the displacement of the stapes fifteen or twenty times, and the leverages of the ossicles in the middle ear will further reduce displacement to the extent of those leverages.

According to the life-sized drawing given by Helmholtz ("Tonempfindungen," p. 190, Ellis tr.), the hinge, *h*, on which the malleus and incus turn is practically in a line with the tip of the incus, *b*, and the lower edge of the stapes, *c* (see Fig. 20). Let *ed* represent the range of the tip of the incus at its junction with the head or os orbiculare of the stapes. Then if we assume a hinge of the stapes at *c*, the motion at the centre of the foot of the stapes, point *g*, will be $\frac{ed \times cg}{bc}$, which would give, according to the scale shown by Helmholtz and assumed to be correct, a leverage of about 2 to 1. Helmholtz states that we have 1½ to 1 leverage due to difference in space moved by tip of malleus and tip of incus, so that we have a combined leverage of 3 to 1 independent of the reduction of displacement due to areas.

As the drum skin is about twenty times the area of the stapedial foot-plate, this would give a total increase of effective pressure of 20 × 3 or 60 to 1. This can only be regarded as an approximate estimate, and on the assumption that no slip occurs at the joint between the malleus and incus and that the hinge, *h*, below this joint, which is formed of elastic ligaments, moves slightly to accommodate itself to the movement of the tip of the stapes, which is in a circular arc round its hinge at *c*. All the displacement which could find its way as units of work into the moving liquid of the cochlea must pass by this route.[1]

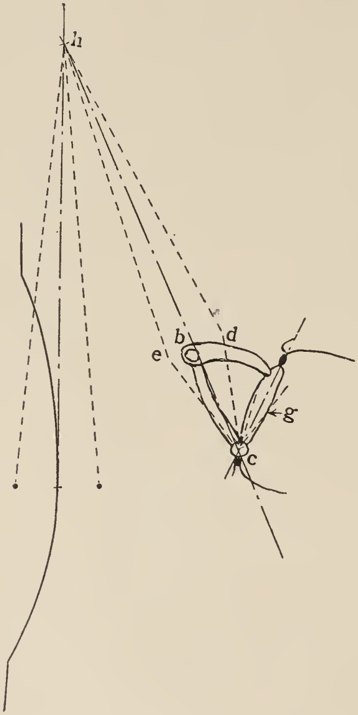

FIG. 20.

The intensifier works also in the opposite direction. When the rarefaction part of the air wave advances on the drum membrane the atmospheric pressure which exists in the middle ear drives the drum membrane backwards.

The malleus and incus are firmly attached to both the drum and the stapes, so that the fenestra ovalis is pulled outwards, and the atmospheric pressure of the middle ear through the fenestra rotunda also follows up the displacement caused by the outward motion of the stapes. We have thus power applied at the stapes to produce a positive to and fro motion of the liquids in the cochlea.

We shall later have to look more closely into the successive changes of displacement and also the units of work passing through the cochlea, but I have mentioned this in connection with the alternate intensifying and reduction of the unit pressure to indicate the similarity between the action of a hydraulic engine and that of the cochlea. This will be more clearly explained when we come to the action of the basilar piston.

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[1] Any increase of pressure in the middle ear due to the bending of the drum membrane between the attachment of the malleus and the periphery of the drum might cause a slight rise of pressure in the middle ear, but such increase would not be transmitted to the stapes as the same rise of pressure acts through the fenestra rotunda, thus balancing that acting on the fenestra ovalis.

The cochlea, which is filled with liquid, consists of a spiral tube somewhat resembling a snail shell winding round a conical cavity. Fig. 21 (Quain's "Anatomy,"

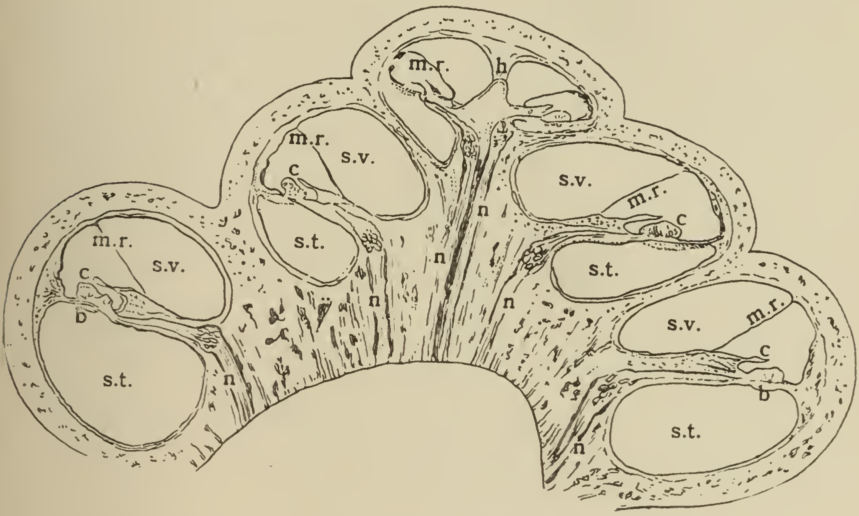

Fig. 21.—Vertical Section of the Cochlea laying open its Passages (Quain).

s.v.	Scala vestibuli.	m.r.	Reissner's membrane.
s.t.	,, tympani.	n.n.n.	Nerve canals on modiolus.
c.	,, media or cochlear canal.	h.	Position of helicotrema.

p. 319), is a diagrammatic section through the cochlea by Schäfer. The perilymph occupies the whole interior of the cochlea, except the scala media (seen as a triangular section in Fig. 21), which contains the organ of Corti, and is filled with a different fluid, the endolymph.

The scala media winds up the spiral of the cochlea in the way shown in Fig. 21, and is separated from the perilymph of the scala vestibuli by the membrane of Reissner, marked *m.r.*, and from the scala tympani by the basilar membrane, marked *b.*[1] As the whole cochlea is full of fluid, and these two membranes serve as partitions between the perilymph and the endolymph, the to and fro motion of the former is not conveyed longitudinally to the endolymph in the scala media in which the delicate nerve terminations lie.

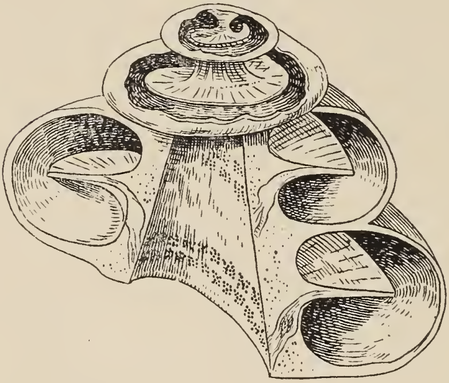

FIG. 22.—SECTION OF THE BONY COCHLEA SHOWING THE CENTRAL CANAL FOR NERVES AND THE BONY SHELF, AT THE OUTER EDGE OF WHICH THE BASILAR MEMBRANE IS ATTACHED. (POIRIER'S "ANATOMY.")

The auditory nerve fibres commence at the sensory cells, situated on or near the bases of the rods of Corti. They are arranged in bundles, approximately 4,000 in number, and pass out from the cochlea at a continuous series of foramina situated near the margin of the basilar membrane.

A section through the central axis of the cochlea (Fig. 22) taken from Poirier's "Anatomy" (p. 1353) shows these minute apertures arranged like a spiral staircase round the central cone of the cochlea. As the nerves from the helicotrema to the base of the cochlea accumulate in the cone, they are passed on in an increasing bundle to the brain. Fig. 23 is a section through the labyrinth, showing how the fenestra ovalis communicates with the vestibular passage above the Reissner membrane, and the route by which the displacements of the liquid of the labyrinth return through the cochlea on the under side of the basilar membrane to the fenestra rotunda. Fig. 24 is an external view of the labyrinth showing the semi-circular canals which were shown by Flourens in 1842 to form an organ enabling us to be conscious of the balance of our movements. This book does not deal with the functions of this part of the labyrinth, which is independent of the cochlea, and which have been investigated by Barany, Crum Brown, and later by Dr. Sydney Scott.

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[1] From the point of view of a physicist it is unnecessary to draw a distinction between the fluids of the cochlea. They may be regarded as one mass filling the interior of the cochlea. In this mass are suspended Reissner's membrane, the basilar membrane, and organ of Corti; these may be regarded as parts of the fluid mass and all partaking in the most delicate movements of displacement.—A. KEITH.

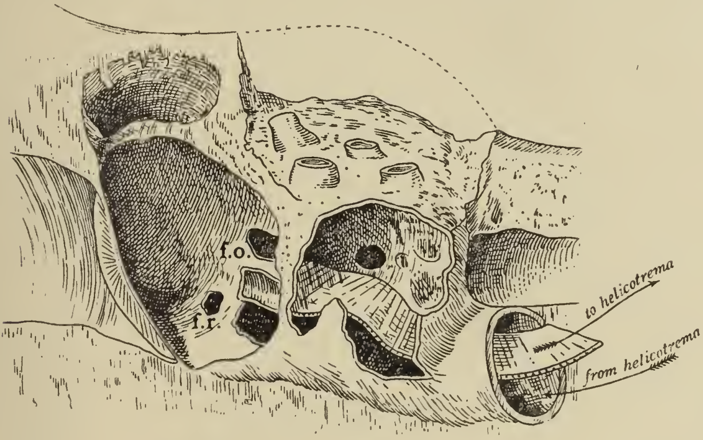

Fig. 23.—Section Exposing the Interior of the Vestibule with the beginning of the Scala Vestibule, and termination of the Scala Tympani. (Poirier.)

f.o. Fenestra ovalis
f.r. Fenestra rotunda
} Seen within tympanic cavity.

Fig. 25, page 55, is a section by Dr. Keith showing the stapes hinged at the entrance to the scala vestibuli.

Fig. 26, page 56, is a section through dotted line in Fig. 25, also by Dr. Keith, showing the fenestra rotunda at the termination of the scala tympani, also the commencement of the scala vestibuli with the stapes at its entrance.

Fig. 27, page 57, is a cross section by Dr. Keith of the second turn of the cochlea magnified 60 times, showing the two scalæ filled with perilymph and the scala media or scala cochlea filled with endolymph, a fluid of different constitution from the perilymph; these liquids are separated by the basilar membrane at the lower and by Reissner's membrane at the upper boundary of the scala media.

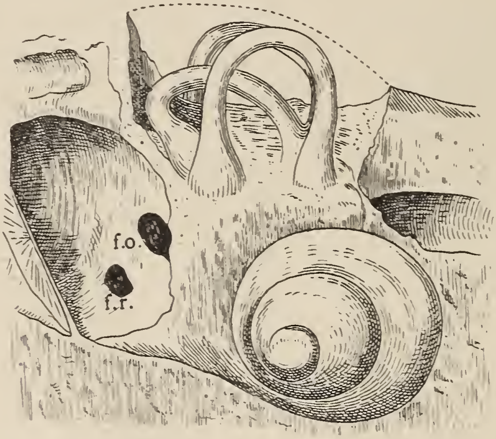

Fig. 24.—The Bony Cochlea and Semicircular Canals of the Right Side, the Apex or Cupola of the Cochlea being directed towards the Spectator.

The cavity of the tympanum is exposed, showing the fenestra rotunda and fenestra ovalis.

The organ of Corti is shown in the same figure resting on the basilar membrane, and the tectorial membrane resting on the hairlets at the top of the organ of Corti.

With regard to reductions of amplitude, Politzer "Diseases of the Ear") quotes the experiment of Buck), which proved that—

"The greatest excursions observed at the extremity of the manubrium of the malleus were 0·76 mm., those of the long process of the incus 0·21 mm., and according to

Helmholtz, those of the stapes 1/18th to 1/14th mm., or a mean of 0·06 mm. These measurements are, however, the result of extreme excursions of the ossicles, brought about by alternate condensations and rarefactions of the air in the external meatus or in the tympanic cavity. On the other hand, during vibrations caused by sound, the excursions of the stapes are limited (Gelle) ; and Reimann justly states that with weak but still plainly perceptible tones, these motions of the stapes must be so small that they cannot be seen even with the most powerful microscope."

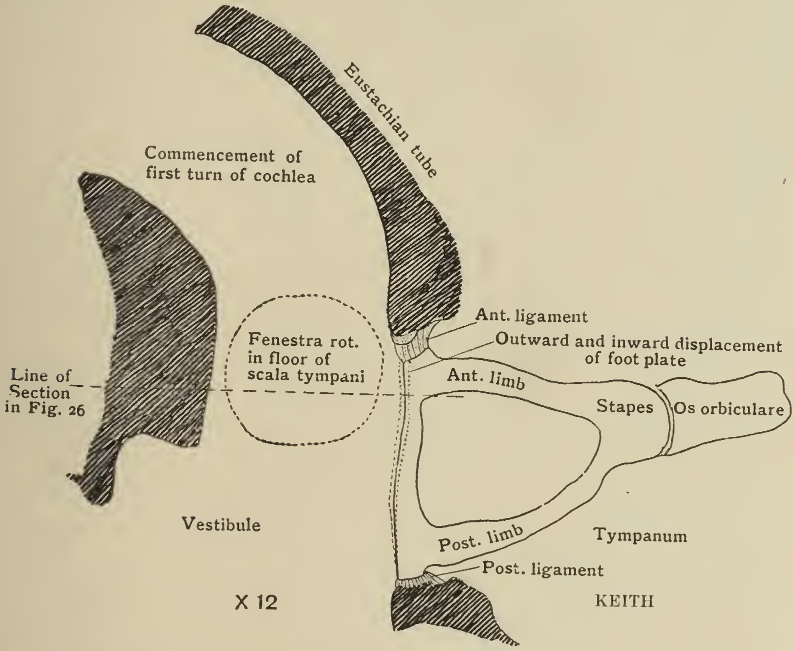
Eustachian tube
Commencement of first turn of cochlea
Fenestra rot. in floor of scala tympani
Line of Section in Fig. 26
Ant. ligament
Outward and inward displacement of foot plate
Ant. limb
Stapes
Os orbiculare
Vestibule
Post. limb
Tympanum
Post. ligament
X 12
KEITH

FIG. 25.—HORIZONTAL SECTION ACROSS THE FENESTRA OVALIS AND VESTIBULE, TO SHOW THE RELATION OF THE STAPEDIAL FOOT-PLATE TO THE BEGINNING AND END OF THE COCHLEAR PASSAGES.

It is difficult to realise that these minute motions can be ordinary molar motions, but we have a proof supplied in the action of the phonograph. In this instrument the almost microscopic groove upon the wax of the receiver cylinder caused by the mechanical vibration of one membrane is made to deliver up to a second membrane an almost exact imitation of the vibration of the first which produced the grooves in the wax. Molar motion is clearly the cause of the reproduction, and therefore it is reasonable to regard it as being the cause of the production.[1]

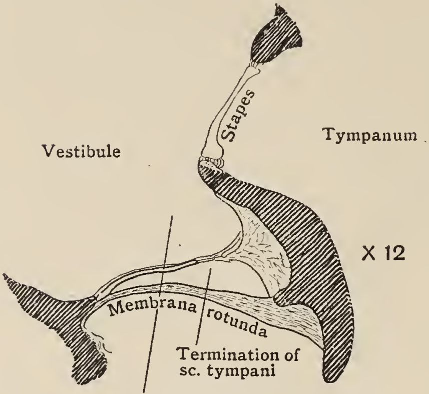

FIG. 26.—VERTICAL SECTION OF THE PARTS SHOWN IN FIG. 25. THE SECTION SHOWS THE MEMBRANE CLOSING THE FENESTRA ROTUNDA.

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[1] In this hypothesis, I accept the views of Helmholtz to be correct as given in his "Mechanism of the Ossicles," published by the New Sydenham Society, 1874, p. 106, and which is translated as follows:—"An incompressible fluid contained between solid walls is distinguishable from a compressible one in this: that every impulse which reaches any part of its surface communicates itself immediately throughout the whole fluid and sets every part instantly in motion, while in a compressible fluid a wave proceeds from the spot of action and travels with a certain velocity, setting in motion the several particles of the fluid consecutively. Thus if the dimensions of the whole mass are infinitely small in comparison with the wave-length (as it is in the labyrinth water), and if the walls of the petrous bone which enclose it are so solid that we can consider them as absolutely so when compared with the minute pressure under consideration, we deduce the following: The communication of action throughout the whole mass is practically instantaneous, and the labyrinth water under the influence of the sound waves moves virtually as a fluid absolutely incompressible (and therefore incapable of sound waves) would move under the same relations."

Professor Bezold, of Munich, writing on bone conduction, "Archives of Otology," New York, says: "I share the conviction of all physiologists and otologists that not molecular movements but mass movements of the conducting chain, together with the labyrinth water column, transmit the sound waves from the air. Accepting this, we cannot recognise that the nerve terminals are also attacked by molecular vibrations, which most authors assume to be present in the form of direct transmission through bone. I am, moreover, on the side of those physiologists who regard bone conduction as osteo-tympanic—in other words, in conduction through bone the excitation of the auditory nerve takes place exclusively with the aid of the sound conducting apparatus vibrating with the bone."

In order to conceive how such vibrations can be communicated to the nerves of hearing without disturbing

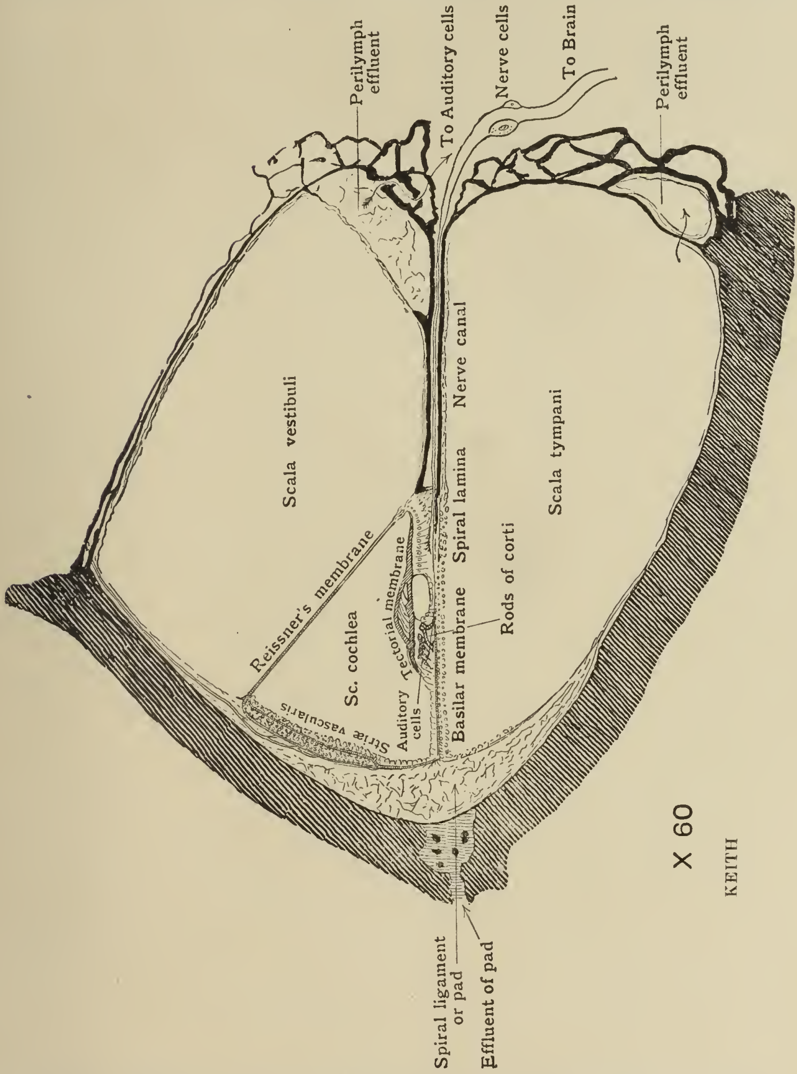

Fig. 27.—Section across the Middle Turn of the Cochlea, to show the Position and Relationship of the Organ of Corti to the Various Scalæ of the Cochlea.

the impulse points of each wave, let us take a tube of glass, such as shown below (Fig. 28), tapered towards the

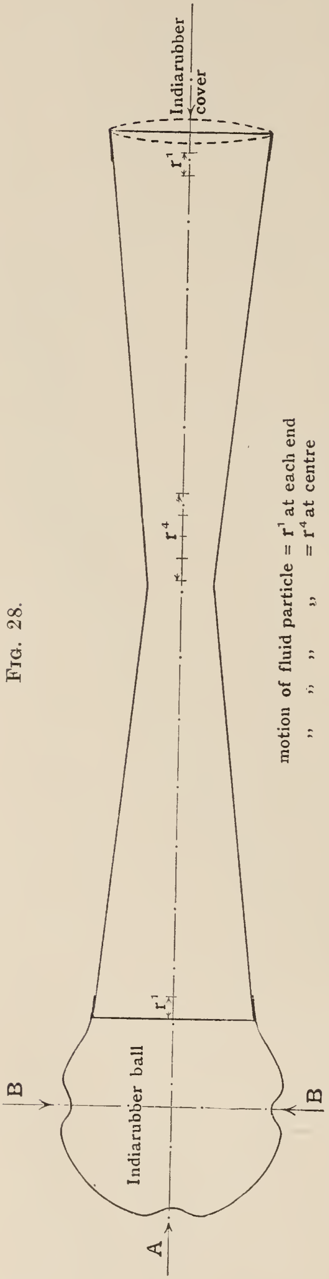

Fig. 28.

middle of its length, with an indiarubber ball at one end, and an elastic flat membrane at the opposite end, and fill the whole tube with liquid; a pressure of the finger into the indiarubber ball causes the water to move in mass along the whole length of the tube, and the flat membrane moves out with a cubical displacement equal to the displacement at the ball.

If the glass tube were equal in diameter in its whole length, the to and fro motion of each particle of water (disregarding the effect of surface friction) would have the same range and the same velocity. If, however, the glass tube be reduced, as in this case, for a portion of its length in the middle to one-half the diameter or one-fourth the area at the ends, the velocity of each particle of water will have to adjust itself to the sectional area it is at the moment passing, and the velocities will be in inverse ratios to those areas; in this case the area of the tube is four times greater at the ends than at the middle, and the to and fro range of each particle of liquid will at any one section of the tube be greater in the inverse ratio of the areas; *but the period of the impulses will remain the same.* This appears to represent the conditions of the cochlea of the ear. The passage decreases in area from the fenestra ovalis to the helicotrema, and then increases again down to the fenestra rotunda.

The pressure forward, as at arrow *A*, on the indiarubber ball in line with the axis of the tube represents the impulse given to the liquid of the cochlea by the direct action of the stapes.

A transverse squeeze, as at arrows *B*, given to the indiarubber ball represents a transverse motion, to which attention will be called later. Both direct and transverse impulses are converted into longitudinal mass movements of the liquid in their passage to the fenestra rotunda.

It is obvious that a gradual increase in the velocity of each particle of perilymph will take place as it passes over diminishing sections nearer and nearer to the helicotrema, and that these will decrease in velocity gradually as the liquid passes increasing sections from the helicotrema to the fenestra rotunda.

In the next chapter we will examine the nature of these varying velocities and the impulses due to the cessations and reversals of the liquid in the passages of the cochlea and how these velocities and impulses are transmitted to the nerve terminations in the endolymph of the scala media.

ADDENDUM TO CHAPTER II,

CONTAINING PARTICULARS OF IMPULSES SHOWN BY DIAGRAMS FOR DIFFERENT MUSICAL INTERVALS AS PREVIOUSLY PUBLISHED, 1907.

Octave C, C¹. Musical notation.

DIAGRAM 1. Gives wave form of an octave 1 : 2 ratio, amplitude equal, 3 varying phases.

DIAGRAM 2. Gives wave form of octave—

Amplitude	.. ..	12 : 7
Ratio ..	.. ..	1 : 2

Starting in same phase.

DIAGRAM 3. Gives wave form of octave—

Amplitude	.. ..	12 : 7
Ratio ..	.. ..	1 : 2

Starting phase ½ circle in advance.

DIAGRAM 4. Gives wave form of octave—

Amplitude	.. ..	12 : 7
Ratio ..	.. ..	1 : 2

Phase ¾ advance.

The octave is a perfect interval according to the hypothesis, because in whatever condition of amplitude or phase, it will be seen that all the maxima, minima and crossing points are effective for production of the original tones.

Perfect Fifth. (C, G, Musical notation.)

DIAGRAM 5. Ratio .. .. .. 2 : 3

Equal amplitude—phases starting together.

Diagrams 6 and 6a. Equal amplitude—varying phases.

In diagram 5, out of 12 maxima, minima and crossing points, 11 are effective.

In diagram 6, out of 12 maxima, minima and crossing points, 11 are effective (some of which are common to both notes), 4 are effective for C, and all points for octave below C (which indicates the differential tone in this interval).

8 are effective for G.

In 6a there are, owing to change of phase, only 10 maxima, minima and crossing points. Out of these 7 are effective.

6 are effective for C,
2 are effective for G,

and all points are effective for octave below C, which is the differential tone.

The 5 spaces *s*, *s*, *s*, *s*, *s*, etc., dividing the cycle into 5 equal parts, indicate the summational tone.

Perfect Fifth with variations of amplitude.

(C, G, Musical notation.)

Diagram 7. Ratio .. 2 : 3
Amplitude 14 : 9—Phases starting opposite.

Out of 10 maxima, minima and crossing points, 8 are effective.

3 are effective for G,
6 are effective for C,

and all points are effective for octave below C (being differential tone). Points *s*, *s*, *s*, *s*, *s* are effective for summational tone (2 + 3).

Diagram 7a. Ratio .. ... 2 : 3
Amplitude .. 14 : 9
Phases slightly different from Diagram 7.

Out of 9 maxima, minima and crossing points, 7 are effective.

4 are effective for G,
4 are effective for C,

and all points are effective for octave below C (being differential tone). Points *s*, *s*, *s*, *s*, *s* are effective for summational tone.

DIAGRAM 8. Ratio .. .. 2 : 3
Amplitude .. 19 : 24

Phases starting together.

Out of 12 maxima, minima and crossing points, 5 are effective.

2 are effective for C, and all for octave below C (being the differential tone).
4 are effective for G.

Points s, s, s^1, s^1, s^2, s^2, s^3, s^3 are effective for summational tone in four different systems.

DIAGRAM 8A. Ratio .. .. 2 : 3
Amplitude .. 19 : 24

Phase of high note varied.

Out of 12 maxima, minima and crossing points 9 are effective.

6 are effective for G,
4 are effective for C,

and all points for octave below C—s^1, s^1, s^1, s^1, s^1, and s^2, s^2—are effective for summational tone.

Perfect Fourth. (C, F.)

DIAGRAM 9. Ratio .. .. 3 : 4
Equal amplitude.

Phases commencing together.

Out of 14 maxima, minima and crossing points, 13 are effective and 1 a close approximation (including the octaves below the primaries marked 2 C and 2 F). The octave below F is in this interval the differential.

It will be noticed that the impulse points representing F are all an octave below that note. This may account for the peculiar character of this interval.

DIAGRAMS 10 AND 10A.
Ratio .. .. 3 : 4
Equal amplitude.
Varying phases.

In diagram 10, out of 14 maxima, minima and crossing points, 12 are effective.

In diagram 10A, out of 16 maxima, minima and crossing points, 13 are effective—s^1, s^1, s^1—s^2, s^2, and s^3, s^3 in 3 different systems are impulses for summational tone.

DIAGRAM 11. Ratio .. .. 3 : 4
Equal amplitude.
Phase varied.

Out of 14 maxima, minima and crossing points, 12 are effective or close approximation.

DIAGRAM 12. Ratio .. .. 3 : 4
Amplitude .. 8 : 5
Phase varied.

Out of 12 maxima, minima and crossing points, 7 are effective.

2 are effective for F.
6 are effective for C.
6 for octaves below C.

s^1, s^1 ,s^1, s^1—s^2, s^2—s^3, s^3 in 3 different systems are effective for summational tone.

DIAGRAM 13. Ratio .. .. 3 : 4
Amplitude .. 8 : 5
Phase varied from diagram 12.

Out of 13 maxima, minima and crossing points, 8 are effective, and s^1, s^1—s^2, s^2 and s^3, s^3 effective for summational tone.

Major Sixth. (C, A.)

Diagram 14. Ratio .. .. 3 : 5
Amplitude equal.

Phases commencing together.

Out of 20 maxima, minima and crossing points, 16 are effective.

Summational tone 5 + 3 indicated by impulses *s*, *s*, *s*, etc., equidistant.

Diagram 15. Ratio .. .. 3 : 5
Amplitude equal.

Phase varies from diagram 14.

Out of 20 maxima, minima and crossing points, 19 are effective.

That marked x only being non-periodic. The points *s*, *s*, *s*, etc., indicate the summational tone impulses, the distance apart being $\frac{1}{3+5}$ or one-eighth of the whole cycle.

Diagram 16. Ratio .. .. 3 : 5
Amplitude equal.

Phase varied from diagrams 14 and 15.

Out of 16 maxima, minima and crossing points, 14 are effective, those marked x and x being the only non-periodic impulses and they coincide with the summational impulses.

Diagram 17. Ratio .. .. 3 : 5
Amplitude equal.

Phase varied from diagrams 14, 15 and 16.

Out of 16 maxima, minima and crossing points, 12 are effective, those four marked x being non-periodic, and one of these is effective for the differential tone as explained in diagram.

Diagram 18. Ratio .. .. 3 : 5
Amplitude .. 2 : 1

Phase of higher note $\frac{1}{4}$ in advance.

Out of 15 maxima, minima and crossing points, 15 are effective.

The points *s*, *s*, *s*, etc., in this case appear to coincide with maxima and minima, and not with crossing points. The distance apart being $\frac{1}{3+5}$ or one-eighth of the whole cycle.

Diagram 19. Ratio .. .. 3 : 5
Amplitude .. 8 : 13

Out of 15 maxima, minima and crossing points, 11 are effective.

The three marked x being the only non-periodic impulses, and of these two coincide with summational impulses.

Major Third.

Diagram 20. Ratio .. .. 4 : 5
Amplitude equal.

Phases commencing together.

Out of 20 maxima, minima and crossing points, 13 are effective, and 9 points *s*, *s*, *s*, etc., indicating summational tone, are practically equidistant, and points s^1, s^1, s^2, s^2 form additional impulses in different systems.

Diagram 21. Ratio .. .. 4 : 5
Amplitude equal.

Phase varied from diagram 20.

Out of 18 maxima, minima and crossing points, 14 are effective, including the octave below each tone, 9 crossing points *s*, *s*, *s*, etc., nearly equidistant indicate summational tone 4 + 5 = 9.

The differential tone 5 − 4 = 1 is produced once in each cycle by *every* impulse.

DIAGRAM 22. Ratio .. .. 4 : 5
Amplitude equal.

Phase varied from diagrams 20 and 21.

Out of 18 maxima, minima and crossing points, 14 are effective.

The 9 crossing points representing the summational tone are practically equidistant.

DIAGRAM 23. Ratio .. .. 4 : 5
Amplitude equal.

Phase varied from diagrams 20, 21 and 22.

Out of 18 maxima, minima and crossing points, 15 are effective, s^1, s^1, etc., equidistant for summational tone, disappearing near the wave of least amplitude.

DIAGRAM 24. Ratio .. .. 4 : 5
Amplitude equal.

Phase varied from diagrams 20 to 23.

Out of 18 maxima, minima and crossing points, 16 are effective.

The 9 crossing points representing summational tone are practically equidistant, except a slight deviation at points *s*, *s*, *s* on flat part of curve.

DIAGRAM 25. Ratio .. .. 4 : 5
Amplitude .. 2 : 1

Out of 17 maxima, minima and crossing points, 13 are effective.

Minor Third. (C, E♭.)

DIAGRAM 27. Ratio .. .. 5 : 6
Amplitude equal.

Phases starting together.

Out of 22 maxima, minima and crossing points, 15 are effective.

s, *s*, *s*, etc., indicate impulses producing summational tones disappearing near the wave of least amplitude.

DIAGRAM 28. Ratio .. .. 5 : 6
Amplitude equal.

Phase varied from diagram 27.

Out of 22 maxima, minima and crossing points, 13 are effective.

Also s^1, s^1, s^1—s^2, s^2, s^2, s^2—s^3, s^3, s^3 in three systems, indicating summational tone impulses.

DIAGRAM 29. Ratio .. .. 5 : 6
Amplitude equal.

Phase varied from diagrams 27 and 28.

Out of 24 maxima, minima and crossing points, 17 are effective.

Also s^1, s^1 ,s^1, s^1—s^2, s^2, s^2, s^2, s^2 effective for summational tone.

DIAGRAM 30. Ratio .. .. 5 : 6
Amplitude .. 2 : 1

Out of 20 maxima, minima and crossing points, 19 are effective.

Also s^1, s^1, s^1, s^1—s^2, s^2 in two systems indicate summational tone.

Minor Seventh. (C, B♭.)

DIAGRAM 31. Ratio .. .. 4 : 7
Amplitude equal.

Out of 28 maxima, minima and crossing points, 21 are effective.

DIAGRAM 32. Ratio .. .. 4 : 7
Amplitude .. 12 : 7

Out of 20 maxima, minima and crossing points, 20 are effective.

DIAGRAM 33. Ratio .. .. 4 : 7
Amplitude .. 7 : 6

Phase varied from 32.

Out of 26 maxima, minima and crossing points, 20 are effective.

Augmented Fourth. (C, F♯.)

DIAGRAM 34. Ratio .. .. 5 : 7
Amplitude equal.

Out of 24 maxima, minima and crossing points, 20 are effective.

DIAGRAM 35. Ratio .. .. 5 : 7
Amplitude .. 2 : 1

Phase varied from 34.

Out of 20 maxima, minima and crossing points, 17 are effective.

DIAGRAM 36. Ratio .. .. 5 : 7
Amplitude .. 3 : 2

Phase varied from 35.

Out of 20 maxima, minima and crossing points, 16 are effective.

Also s^1, s^1, s^1, s^1, s^1—and s^2, s^2 indicate summational tone.

DIAGRAM 37. Ratio .. .. 5 : 7
Amplitude .. 3 : 2

Phase varied from 36.

Out of 24 maxima, minima and crossing points, 18 are effective.

Minor Sixth. (C, A♭.)

DIAGRAM 38. Ratio .. .. 5 : 8
Amplitude equal.

Out of 30 maxima, minima and crossing points, 24 are effective.

Also s^1, s^1, s^1—s^2, s^2, etc., effective for summational tones.

The points D D D on this diagram divide the cycle into three equal spaces representing the differential tone $8 - 5 = 3$.

DIAGRAM 39. Ratio .. .. 5 : 8
Amplitude .. 12 : 7

Out of 23 maxima, minima and crossing points 15 are effective.

Points *s*, *s*, etc., towards centre of cycle are almost exactly periodic and represent summational tone $\frac{1}{5+8}$ of cycle.

DIAGRAM 40. Ratio .. .. 5 : 8
Amplitude .. 12 : 7

Phase varied from 39.

Out of 22 maxima, minima and crossing points, 15 are effective.

s^1, s^1,—s^2, s^2,—s^3, s^3, s^3, s^3 indicate in three systems the summational tone.

Major Second. (C, D.)

DIAGRAM 41. Ratio .. .. 8 : 9
Amplitude equal.

Phases commencing together.

Out of 36 maxima, minima and crossing points, 22 are effective, not including summational impulses.

Spaces, *s*, *s*, etc., are $\frac{1}{8+9}$ of the whole cycle and indicate the summational tone in several systems.

Dissonant Interval between Major Second and Minor Third.

DIAGRAM 42. Ratio .. .. 6 : 7
Amplitude .. 12 : 7

Out of 24 maxima, minima and crossing points, 10 are effective, and 14 produce noise, hence the inharmonic character of the interval.

Also *s*, *s*, etc., in five systems indicate a summational tone, the distance between each being $\frac{1}{6+7}$ or 1/13th of whole cycle.

Triple Compound. (C, E, G, Musical notation.)
CHORD of th $\frac{5}{3}$

FIG. 18 in paper.

Ratio .. .. 4 : 5 : 6

Amplitude equal.

Out of 24 maxima, minima and crossing points, 19 are effective, viz. :—

11 for C,
8 ,, E,
9 ,, G,

several impulses being common to all three systems.

Five points x being non-periodic.

FIG. 19 in paper. The same chord as above, but with the G moved $\frac{1}{2}$ wave length forward.

Out of 20 maxima, minima and crossing points, 15 are effective, viz. :—

8 for C,
13 ,, E,
9 ,, G,

several impulses being common to all three systems.

NOTE.—The two diagrams, 18 and 19, were plotted by a draughtsman from curves of sines, and not made by the ohmograph.

FIG. 20 in paper. Compound of 4 notes C, E, G, B♭ (chord of minor seventh).

Out of 28 maxima, minima and crossing points, 26 are effective, viz. :—

8 for C
15 ,, E
8 ,, G
6 ,, B♭

Several being common to all systems,

two impulse points, x, x, only being non-periodic to any of the four systems.

TABLE SHOWING PERCENTAGES OF HARMONIOUS IMPULSES IN THE DIAGRAMS OF MUSICAL INTERVALS.

	Diagram.	Effective Impulses.	Percentage.	Mean Percentage.
Octave	1 to 4	All	100	100%
Perfect Fifth ... ... 2 : 3	5	11 out of 12	92 $\frac{254}{3}$	85%
	6	11 ,, 12	92	
	6A	7 ,, 10	70	
Do. with Large variations in amplitude	7	8 ,, 10	80 $\frac{275}{4}$	69%
	7A	7 ,, 9	78	
	8	5 ,, 12	42	
	8A	9 ,, 12	75	
Perfect Fourth ... ... 3 : 4	9	13 ,, 14	93 $\frac{465}{6}$	77%
	10	12 ,, 14	86	
	10A	13 ,, 16	81	
	11	12 ,, 14	86	
	12	7 ,, 12	58	
	13	8 ,, 13	61	
Major Sixth ... ... 3 : 5	14	16 ,, 20	80 $\frac{510}{6}$	85%
	15	19 ,, 20	95	
	16	14 ,, 16	87	
	17	12 ,, 16	75	
	18	15 ,, 15	100	
	19	11 ,, 15	73	
			or without 18 $\frac{410}{5}$	82%
Major Third .. ... 4 : 5	20	13 ,, 20	65 $\frac{471}{6}$	78·5%
	21	14 ,, 18	78	
	22	14 ,, 18	78	
	23	15 ,, 18	83	
	24	16 ,, 18	90	
	25	13 ,, 17	77	
Minor Third ... ... 5 : 6	27	15 ,, 22	68 $\frac{293}{4}$	73%
	28	13 ,, 22	59	
	29	17 ,, 24	71	
	30	19 ,, 20	95	
Minor Seventh ... ... 4 : 7	31	21 ,, 28	75 $\frac{252}{3}$	84%
	32	20 ,, 20	100	
	33	20 ,, 26	77	
			or omitting 32	76%
Augmented Fourth ... 5 : 7	34	20 ,, 24	83 $\frac{323}{4}$	81%
	35	17 ,, 20	85	
	36	16 ,, 20	80	
	37	18 ,, 24	75	
Minor Sixth ... ... 5 : 8	38	24 ,, 30	80 $\frac{213}{3}$	71%
	39	15 ,, 23	65	
	40	15 ,, 22	68	
Major Second ... ... 8 : 9	41	22 ,, 36	61	61%
Dissonant Interval between Major Second and Minor Third ... ... 6 : 7	42	10 ,, 24	42	42%
Triple compound	Chord of $\frac{5}{3}$ musical notation C, E, G.			
	Fig. 18 in paper	19 out of 24	79 $\frac{154}{2}$	77%
Do. with G curve moved forward ½ wave-length...	Fig. 19 in paper	15 ,, 20	75	
Compound of four notes, Chord of the minor seventh, C, E, G, B♭ ...	Fig. 20 in paper	26 ,, 28	93%	93%

CHAPTER III

CALIBRATION OF THE COCHLEA AND ITS EFFECT ON THE LABYRINTH IMPULSES WITH THEIR CONVERSION INTO NERVE STIMULI

If we regard the motion of the particles of the perilymph as capable of transmitting, directly or indirectly, an excitement, tactile or mechanical in character, on the 15,000 or 20,000 sensory or hair cells of the organ of Corti, which are, according to Koelliker and other observers, spread out in files of four or five deep in a long spiral band, on the surface of the Corti organ above the basilar membrane, we must see how important to our perception of hearing will be the character of the tactile effect produced.

When, with the forefinger of the right hand, the palm of the left hand is lightly rubbed, very little sensation is conveyed to the brain if the motion of the finger is very small, but if the finger be moved over one or two inches with the slightest touch, the sensation sent to the brain is very considerable, because the forefinger is exciting a larger number of nerve terminals.

Hence the necessity (if audition be regarded as being in the nature of a tactile sense) that in the auditory apparatus the nerve terminations should also be spread out in an extended line to meet the requirements of tactile perception.[1]

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[1] The strength of stimuli depends not only on the number of nerve terminals touched or concerned, but also on the intensity of the force applied.—A. Keith.

The energies of these tactile motions representing loudness and quality of tone are no doubt finally converted into nerve impulses. At present our attention is attracted to the mechanical means by which the motions of the stapes are converted into similar motions in the processes of the hair cells of Corti's organ, which are at present regarded by anatomists and physiologists as the final points, or end-stations, where the motion is converted into nerve stimuli.

The author approaches this subject from the point of view of an engineer who has an intricate machine presented to him which accomplishes certain work, and for which a mechanical explanation is asked.

In a previous chapter he has shown that impulses caused by changes of pressure in the air, which can be shown graphically to exist, correspond with the actual phenomena of compound tones, which appeal to the brain. As our consciousness of these is the best proof that they must have arrived there without confusion, we ought to be able to track the changes in the route as the mechanical motion passes from one medium to another.

The object of this chapter is to follow the molar motions and impulses of the perilymph, and to show what character they assume at each section of the cochlea ; further, how they are conveyed to the Corti arches through the basilar membrane and how modified in their conveyance so that the motions and pressures at the nerve termination are of the same character and in proportion to the motion and pressures at the stapes and basilar membrane, and to identify them with the various phenomena of simple and compound sounds as they appeal to our sensations of pitch, and, at the same time, produce the varying sensations of loudness and timbre or quality of tone.

The simplest form of vibration of an elastic sonorous body is recognised to be of a pendular, or more correctly of a harmonic, character. In the same way as the force of gravity acting on the mass of a pendulum is the cause of the maintenance of its motion, so elasticity in the vibration of a sonorous body is the cause of the maintenance of its vibration.

The surface of the vibrating elastic rod presses the elastic air into successive waves of condensation and rarefaction, which travel forward in a direction at right angles to the motion of the particles in the vibrating bar until they arrive at the outer membrane of the ear. The motion is then passed by the ossicles, which form a series of articulated levers, to the stapes and the attached membrane of the fenestra ovalis of the cochlea, multiplying the pressure as described on p. 47. Here the motion of each increment of displacement is propagated through the liquids in the cochlea instantaneously to the fenestra rotunda[1] on its way through the basilar membrane.

The three membranes move together ; in fact, they may be regarded as a threefold membrane vibrating system with the intermediate fluid (which is constant in volume filling the whole interior) moving between and along with the membranes.

If the passages of the cochlea were uniform in sectional area between the membranes, the longitudinal movement of each particle of liquid would be the same in character as the movement of the membranes.

This, however, is not the case, as the areas of both passages are reduced as they converge towards the helicotrema, so that the velocity of each particle of fluid must be increased or decreased in comparison with the velocity at the front of the stapes.

It is well here to state generally the principle upon which mathematicians have arrived at the conventional forms expressing the passage of sound waves in air.

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[1] In Helmholtz's "Mechanism of the Ossicles," he states : "The communication of action throughout the whole mass is practically instantaneous, and the labyrinth water, under the influence of the sound waves, moves virtually as a fluid absolutely incompressible would move under the same relation."

Take an air displacement curve as below, Fig. 29. Let *A*, *B* be the direction of propagation. Let *C*, *D*, *E*, *F*, *G* be the original undisturbed positions of certain air particles. While the wave is passing let the air particles *D*, *E*, *F* be moved into positions *d*, *e*, *f*, then if the vertical ordinates be drawn on *D*, *E*, *F*, etc., in proportion to the displacements of the air particles *D d*, *E e*, and *F f*, etc., a sine curve can be constructed which conventionally describes the form of the wave. At *G* the particle is at the moment undisturbed.

In the rarefied portion of the air wave passing on between *G* and *M*, the particles *H*, *K*, *L* take up the positions *h*, *k*, *l*, and *M* is at the moment undisturbed.

It is evident that there is a crushing in of the air particles between *E* and *K*, and a retreat from each other of the particles between *K*, *M* and *C*, *E*. Hence the elastic reaction and therefore the pressure and velocity are greater in the former and less in the latter, the maxima and minima of pressure being respectively at the crossing points and crests or hollows of the air displacement curve. (See Poynting and Thompson's "Text Book of Physics in Sound," p. 12, 1899.)

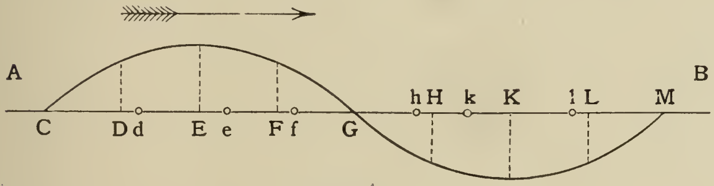

FIG. 29.

This causes a change in the successive time positions of pressure, and in the conventional pressure and velocity air curve the maximum pressure corresponds in time with the minimum displacement of the air particles, while the minimum pressure coincides with the maximum displacement, and the air pressure curve is $\frac{1}{4}$ wave-length in front of the air displacement curve.

We have now to consider how the varying pressures in the air displacement curve affect the movements of the stapes where the elastic movements of the air are converted into the mass movements of the liquid.

Let Fig. 30 represent the relations between the piston (stapes) and the curves of air displacement and air pressure, the former curve in dotted lines, the latter in full lines.

Let *a*, *b*, *c* represent positions of the stapes as it moves from its extreme outward and inward positions through its

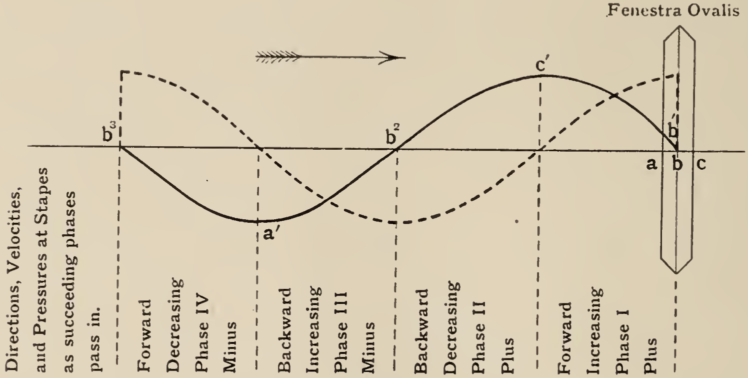

Fig. 30.

central position, *b*, the corresponding points in the curves being marked with similar letters to suit the successive times of arrival at the stapes.

b is the natural resting position of the piston being pulled in by the tension on the tensor tympani and pulled out by the stapedius, there being in this position of rest equal tension on both muscles (see p. 40).

When *b′* in air *pressure* curve shown in full lines arrives at *b*, the increasing pressure as shown between *b′* and *c′*, Phase I, in the curve, forces the piston to *c*, gradually putting an increased tension on the ossicular muscles, until the tension balances the pressure of the wave at *c′*, when motion of the stapes ceases at *c*.

As the wave continues to advance, the pressure between c' and b^2, Phase II, diminishes gradually, and as this takes place the ossicular muscles relax their tension and exercise their potential energy upon the piston, which, having reversed, again arrives at b.

The rarefaction of the sound wave then sets in, and as that part of the wave passes in from b^2 to a', Phase III, the piston moves back from b to a, putting an increased tension on the ossicular muscles until the tension balances the rarefaction of the wave at a'. At this point the rarefaction is at its maximum and the piston just about to reverse.

The curve between a' and b^3, Phase IV, then decreases in rarefaction, and as this takes place the ossicular muscles relax their tension and the piston again arrives at b. This completes the cycle. As the relaxation of the muscles is controlled by and only takes place in consequence of the decreasing pressure of the wave form (either positive or negative), allowing the piston to come forward or backward, it will be seen that the motion of the membrane is dead beat in its character, being controlled by the non-elastic liquid at the other side of the stapes.

The air displacement dotted curve, representing a conventional displacement of the particles of the elastic air, ceases to have any signification when the pressures resulting from them are passed into a liquid medium which is not elastic, the particles of which, at the low pressures now being considered, neither approach nor retreat from each other, but are mobile and able to adapt themselves as a whole to whatever shape the vessel may be into which they are pressed. It will be observed that the displacement of liquid becomes a cubical displacement and not a linear displacement of particles as in the air pressure curve. From these considerations it will be recognised that, although the curve representing time-pressure in a sound wave also represents velocity when the tube is uniform in area, it does not represent velocity when the tube varies in area. We must therefore follow the pressure curve as shown in the full lines of Fig. 30, after passing into the liquid medium, where the successive pressures are exerted in every direction regardless of the shape of the vessel.

Let us suppose the cochlea to be a tube of uniform diameter with a piston of the same area at each end, the left-hand piston receiving the intensified pressure of the air wave, and the right-hand piston carrying out of the system the pressures to produce external mechanical work as we have in a hydraulic engine; then, supposing the whole space between the two equal pistons to be filled with a constant volume of liquid, the two pistons would be moved one with the other over their small range exactly as though connected by a solid attachment from piston to piston. This would hold good irrespective of the length of the tube as compared with the small range of the piston motion; but it also holds good if, between the spaces representing the motion of each piston of equal area, variations are made in the intermediate sectional areas of the tube. A reduction of area would mean that the liquid moves more rapidly, and an increase of area that the liquid moves less rapidly. At every section, velocity multiplied by area will equal a constant, and the mobility of the liquid enables the particles to adjust their positions and velocities so that the whole mass of liquid between the pistons would act as if there were a solid connection between them, always maintaining the same distance between the two equal pistons. The units of pressure delivered by the first piston at any moment of time are carried forward to the other, so that the pressure between the two pistons would rise and fall according to the varying pressures delivered to the left-hand piston as the air wave form arrived.

It is obvious that the same cubical displacement in unit time will occur at each piston, but there will also be the same cubical displacement in unit time for every section between the pistons.

Unit cubical displacement = space moved in unit time × mean area.

When space moved is indefinitely small and difference of area is also indefinitely small,

Space moved in unit time = velocity in unit time.

Therefore unit cubical displacement = unit velocity × area.

If between the pistons velocity is increased by area being diminished in inverse proportion, it is clear that unit cubical displacement is not affected. Therefore the displacement during the same small unit of time is constant throughout the length of the axis of the tube, however its area between the pistons may vary and its consequent velocity be changed. Of course the variations in the velocity of the liquid cause a loss in the effective pressure and therefore a reduction of effective amplitude and pressure in the air wave, but we are only dealing with the actual movements of cubical liquid displacement in each small increment of *effective* pressure causing motion. What is lost in effective pressure cannot, of course, produce motion or displacement.

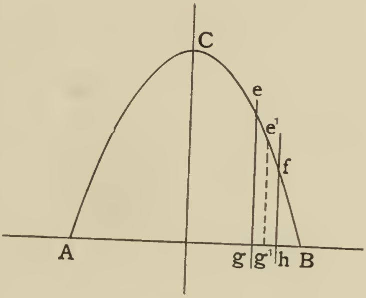

FIG. 31.

The motion of the piston is in point of period exactly equal to the period of the air wave form, although greatly decreased in range.

If in Fig. 31 *A*, *C*, *B* represents the effective pressure wave form in the liquid (*A B* representing time) for movement of the piston during the half-wave, and *g h* represents a small division of time during which the movement of the piston causes a cubic displacement represented by the line *g h*.

In passing through this line the pressure rises from $h\,f$ to $g\,e$.

Then $\dfrac{\text{area } g\,h\,f\,e}{\text{mean pressure}}$ = cu. displacement $g\,h$,

but $$g\,h\,f\,e = \frac{g\,e + h\,f}{2} \times g\,h$$

(regarding $e\,f$ as a straight line); and if the time and displacement become indefinitely small $g\,e$ and $h\,f$ become indefinitely near equality, and at point g^1 the equation becomes

$$\frac{g^1\,e^1 + g^1\,e^1}{2} \times g\,h = g^1\,e^1 \times g\,h,$$

and $g\,h$ being also indefinitely small, the lineal ordinate $g^1\,e^1$ will represent the pressure at g^1.

And for the whole curve $\dfrac{\text{area } A\,C\,B}{\text{mean pressure}}$ = displacement $A\,B$, or area $A\,C\,B$ = mean pressure × displacement $A\,B$. (For further remarks, see p. 92.)

The pressures, as each part of the air wave successively strikes the left-hand piston, run instantaneously through the liquid the whole length of the tube and move the right-hand piston outwards at the same successive pressures and with the same corresponding displacements during the passage of the half-wave form. The above considerations do not take into account the effect of the basilar membrane which will be presently considered.

Before considering the impulses of the liquid movements we must study the compounded effect of stretched elastic bands, when moved from the centre as already described, on p. 40, and illustrated there by Fig. 16.

Let A, C, Fig. 32, represent an elastic band, say 5 inches long when stretched to produce an initial tension of say 5 lb. between A and C. If an additional tension be put on C in the direction of the arrow, the tensions between A and C will rise as the point C passes towards point B as indicated by the vertical lines 5, 6, 7, 8, 9 and 10.

When it arrives at C^1 the tension between A and C^1 will be 1/5th more than when at $C = 6$.

When at C^2 the tension between A and C^2 will be 2/5ths more than when at $C = 7$.

When at C^3 the tension between A and C^3 will be 3/5ths more than when at $C = 8$.

When at C^4 the tension between A and C^4 will be 4/5ths more than when at $C = 9$.

When at C^5 the tension between A and C^5 will be 5/5ths more than when at $C =$ double of original tension.

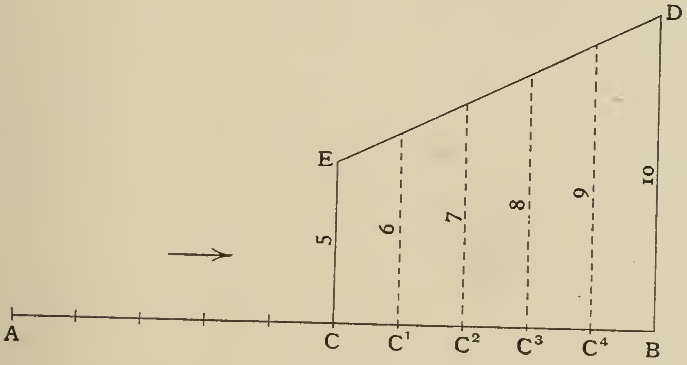

FIG. 32.

This is illustrated in Fig. 33 and is in accordance with Hooke's law of elasticity.

Now take the tension off and let point C^5 return to C, still leaving the initial tension of 5 lb. on A C as indicated in vertical ordinate C, E, above the line, Fig. 33.

Between C and B attach another similar elastic band and pull the whole to a 5 lb. tension and fix the end of the elastic band at B; the point C will not be moved because the new tension on C B balances at point C as soon as it has 5 lb. tension. If with the 5 lb. tension on the whole length we now apply additional pressure in direction of arrow at C the tension of 5 lb. existing in C B may be represented at the under side of Fig. 33, by the vertical line *C F*.

This tension between *C* and *B* will decrease as the point *C* travels towards *B*.

When it arrives at C^1 the tension will be 4
,, ,, C^2 ,, ,, 3
,, ,, C^3 ,, ,, 2
,, ,, C^4 ,, ,, 1

These tensions all assist the moving force to a less and less extent as *C* moves towards *B*.

The real resisting force as the point *C* travels is the difference between the full line ordinates in Fig. 33, above the line, and the ordinates below the line.

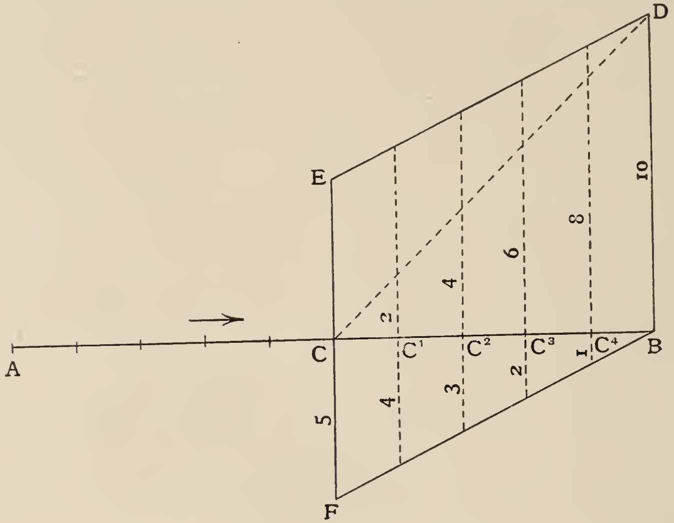

FIG. 33.

These differences are as follows :—

At *C* 5 − 5 = 0
,, C^1 6 − 4 = 2
,, C^2 7 − 3 = 4
,, C^3 8 − 2 = 6
,, C^4 9 − 1 = 8
,, C^5 10 − 0 = 10

These laid down as a series of ordinates in Fig. 33, show that the combined effect of the movement of *C* towards *B* is a uniform increase of tension as indicated by the ordinates of the dotted straight line *C D*.

From the above we see that the resultant of the two elastic resistances which we have in the stapedius and tensor tympani muscles becomes a resistance, commencing at the moment the front of the air wave strikes the piston of the stapes, when in its central position, and that this resultant resistance *C D* in Fig. 33, rises uniformly and in proportion to the space travelled along the line *C B* or *C A*, according to Hooke's law.

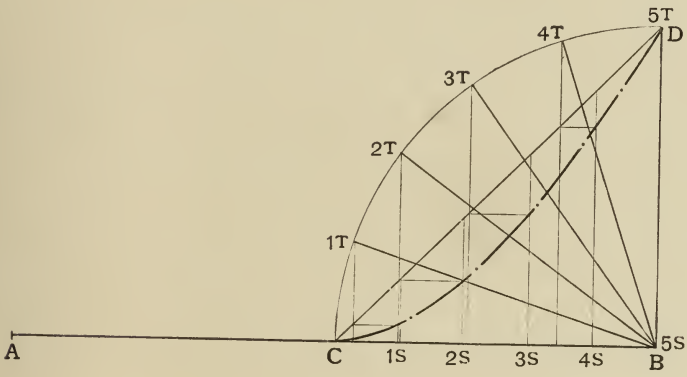

Fig. 34.

It must be observed that Hooke's law of uniform increasing resistance refers to space moved and without reference to time, whereas in the sine curves representing a sound wave it is a diagram of pressures and of time.

To obtain the time curve of the elastic resistances Fig. 34 is constructed.

If upon *B C*, Fig. 34, we show in vertical lines the positions of five equal periods of time and also on the same base *B C* the position of five equal spaces, the former being carried up to a circle passing through equal division of time and marked 1*T*, 2*T*, 3*T*, 4*T*, 5*T*, the equal space divisions being carried through the base line and marked 1*S*, 2*S*, 3*S*, 4*S*, 5*S*, the resistance at any point in a time pressure curve will be represented by the vertical height of the intersection of the sloping line *C D* with the time divisions.

At the central position *C* there is no resistance. At the first time division, No. 1*T*, the resistance is shown by the height of its intersection with the sloping straight line *C D*. This must be the same resistance as at the first space division marked 1*S* on the base line. Therefore if a line parallel to the base line be drawn from this intersection to the No. 1*S* space line, this new intersection will give the first point on the time resistance curve.

In the same way, if from the intersections of the time ordinates 2*T*, 3*T*, 4*T*, with the sloping line *C D*, lines be drawn parallel to *B C* to the space ordinates 2*S*, 3*S*, 4*S*, the intersections on the corresponding space ordinates will produce the dotted curve, the ordinates of which represent the time resistances due to the compound effect of the tensor tympani and the stapedius muscles. The resistance to the horizontal motion at the point *C* thus becomes so minute in short excursions that a membrane or piston fixed at point *C* will convey pressure to a liquid as in the case of the stapes in the cochlea with the greatest efficiency and delicacy as described, p. 40, with illustration of initially stretched indiarubber band, Fig. 16.

We are now able to determine where the chief impulses arise as the to and fro motions of the piston take place.

Upon Fig. 1, Plate V., I have shown a simple air wave, *A*, *B*, *C*, *D*, *E*, approaching the stapes. The total length of the wave form in air corresponds in time to the double stroke of the stapes. Exaggerating the stroke of the stapes in order to get out of microscopic limits and minimising the multiplication of pressure due to lessened displacement, I have made the piston of the stapes to move forward from 0 to 5 (Fig. 2, Plate V, at top of figure); while the air wave travels from *A* to *B* its increasing pressure moves the liquid forward, and the increments of cubical displacement are simultaneously transmitted through the cochlea. The pressure in the air wave plotted on the corresponding time position in the movement of the stapes gives a sine wave between *E* and *F*, though crushed up for the reasons previously given. But the effective forward moving pressure on the liquid is altered by the resistance arising out of the joint action of the stapedius and tensor tympani.

In dotted black lines, phase I, I have shown the time resistance curve due to the joint tension of the ossicular muscles. The pressures indicated by the curved full line *E F* represent in the vertical ordinates positive pressure as the piston passes through the time positions 0—5, increasing in the liquid wave form in the direction of the top arrow. This is reduced by the muscular time resistance shown in dotted lines. There is no moving force at *E* because the air wave at *A* has not commenced to exert a pressure. Neither is there a moving force at *F* when *B* has arrived, because the increase of air wave pressure has ceased and the tension due to the ossicular muscles balances the pressure at *B* in the air wave. The forward moving force at the intermediate time positions is the difference between the vertical ordinates of the pressure curve and the ossicular time resistance curve.

If we, therefore, now plot on the centre line these differences we get the distorted curve shown in red full lines the ordinates of which at each unit of time give the moving force or effective pressure upon the liquid. If we suppose the air wave could be drawn back in the opposite direction after it had pushed the stapes over to *F*, it is obvious that the curve in the cochlea diagram would move back on the same lines as when the wave advanced, and the difference of ordinates between the elastic resistance curve and the pressure curve would be the same at each successive position of the stapes between 5 and 0. In a pure sine curve the back of the wave is symmetrical with the front, and therefore we need no assumption of the air wave moving back. It moves on, but with pressures diminishing as the varying ordinates between *B* and *C* arrive at the stapes in phase II.

The stapes cannot move further to the right of point *F* because the increase of pressure from the air wave has ceased, and it is balanced by the combined pull of the muscles ; so the potential energy in the ossicular muscles follows the piston back upon the rapidly decreasing pressure at the back of the wave form as it advances.

The piston as the back of the wave form, phase II, enters is obliged to retreat as the potential energy of the joint muscular resistance pulls the piston back against the rapidly decreasing pressure at the back of the wave form. If the pressure curve, *E F*, coincided with the resistance curve there would be no movement, but the difference between the positive pressure on the back of the wave form and the negative pull back upon the piston causes the piston to retreat because of the rapid reduction of pressure at the back of the wave form, and when the piston arrives at the central position motion, and therefore momentum ceases.

I have in Fig. 2, Plate V, transferred the point *F* to F^1 below the line, so as to indicate that the motion is now backward, as shown by the lower arrow between F^1 and *E*, or 5 to 10.

Both phase I and phase II are positive in pressure because the positive pressures arising from the sine curve in the air diagram between *A B* and *B C* and also between *E* and *F* or between F^1 and *E* in the liquid diagram are greater in every ordinate until *F* is reached than the opposing resistances acting on the piston of the stapes through the combined resistances of the stapedius and tensor tympani.[1]

The arrival of crossing point *C* in the air wave finds the piston of the stapes at the centre *E*, and the rarefied portion of the air wave begins to flow in. The same reasoning used in the formation of the forward curve marked phase I applies to the formation of the phase marked III, which is negative in pressure, while the piston passes through positions 10 to 15, and the same reasoning applied to phase marked II applies to phase IV, which is also negative in pressure, while the piston is moving through positions 15 to 20. This completes the cycle.

There is thus in a simple wave form a stoppage of motion or cessation of momentum in the whole volume of liquid in the cochlea at the moment when not only the crossing points but the crests of the air wave form arrive at the moving stapes.

It will be observed that the dotted line curve *E F* representing the time resistance of the ossicular muscles is a curve similar to the sine curve of the wave pressures, but reversed.

In other words, the latter takes this form owing to the elasticity of air, the former owing to the elastic resistance of solid in accordance with Hooke's law, but modified from a space pressure curve to a time pressure curve.

If the amplitude of the air wave is increased, the increase will also in the liquid form be carried higher, and as the resistance curve continues in the same line the point where they balance will be further to the right ; in other words, the piston will have a greater travel, which represents increased amplitude or pressure in the air curves and increased displacement in the liquid curve. On Figs.

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[1] The pressure varies as the sine of the angle through which the radius of the generating circle is passing, while the resistance varies as the versine of the same angle. At 0° the sine and versine are both 0, and at 90° they are both 1. In the intermediate angles they differ.

3 and 4, Plate V, are shown diagrams of wave forms equal in period to 1 and 2, but half the amplitude.

The great reduction of displacement through the difference of areas in the drum membrane and the fenestra ovalis, coupled with the further reduction due to the leverages of the ossicles, is necessary in order to increase the unit pressure in the auditory passages to move the mass or weight of liquid in the cochlea, the density and inertia of which are much greater than those of the air. This decrease of displacement means a corresponding increase of pressure and decrease of space moved in unit time, which means also a decrease in velocity when areas are unchanged.[1] This decrease in velocity is desirable in a hydraulic system, as the frictional resistance due to velocity increases as the square of the velocity, and therefore slow moving with high pressure secures the greatest efficiency in this system of motor.

As the motion of the stapes is somewhat complicated, I have made a working model which has been photographed and engraved in Fig. 35.

The bent lever formed by the articulation of the malleus and the incus vibrates on a hinge at *a*. The end of the malleus has a pin *b*, passing through the curved slot in the sliding plate, representing the wave form, so that as the plate moves to and fro, the pin moves towards and from the stapes. And as the hinge *a*, round which the malleus and incus vibrate, is to the left of an imaginary line joining the pin *b* to the stapes, the latter moves in the same direction in which the inclination of the slot obliges the pin to move. When the pin in the malleus is at the axis of the curved slot, as in the drawing, there is an equal initial tension on both tensor tympani and

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[1] If we consider that we have in the liquid of the cochlea a cubical displacement of about one-sixtieth the cubical displacement of the air wave and therefore 60 times the pressure and one-sixtieth of the movement and velocity, we see that Dr. Thomas Young was not far from the truth in representing sound wave forms in straight lines. The sine curve made 60 times higher and its base reduced to one-sixtieth would be a close approach to a triangular formation.

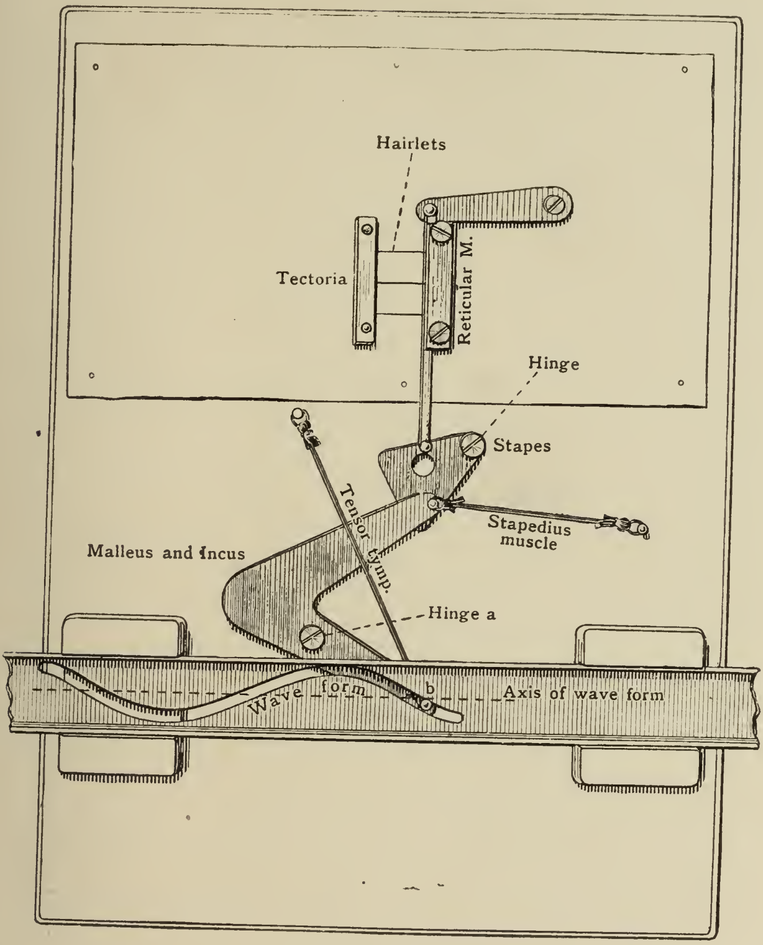

FIG. 35.

stapedius muscles, and therefore the stapes is in its central position. As the movement of the sliding plate causes the pin to move towards the stapes, the tension in the tensor tympani is relaxed, and the tension in the stapedius is increased, until the pin is raised to the highest point of the curved slot. After this point is reached, the descending gradient of the curve reverses the motion of the pin, and the elastic tension on the tensor tympani is increased, and that on the stapedius gives out its potential energy in pulling out the stapes which moves through a small angle round the hinge at its foot. A small connecting rod is shown in the model to move the reticular membrane with the stapes. In the ear this is done, not with any solid connection, but by the displacement of liquid, which, as I have shown, is equally effective. As this motion of the reticular membrane takes place, the hairlets are bent to and fro, as very clearly shown in the model.

We have now to consider the effect of the varying pressures of air arriving through the ossicles at the piston (stapes) upon the liquid at the other side.

Let us imagine a cylinder with a piston on the right side of which is liquid and on the left side air at a certain unit pressure, p, per unit of area.

Then the area × p = total pressure tending to move the piston to the right if there were no frictional or other resistances in the liquid. But if there be resistances, these must be overcome before motion can take place.

If p' = total unit resistance during any small unit of time, then p minus p' represents the moving force, but as the cubical displacement of the piston in unit time (that is the area multiplied by space moved through) is the same as the displacement of the liquid, the effective unit pressure of the liquid displaced is lowered by the amount of the unit resistance, p'. Hence this resistance has the effect of decreasing the effective ordinates of the air curve representing pressure, so that if the ordinates of a sine curve represent the successive pressures in the free air curve, the successive increments of pressure which pass instantaneously through the liquid of the cochlea would be represented by a curve of diminished amplitude, the diminution representing at each time position the changing values of p'.[1]

In the small space moved by the surface of a steel vibrating bar producing a pure tone the momentum or work done in any complete vibration is passed on to the elastic air in the form of a simple pulsation; but as the air has so much less mass and density than the steel, each particle of air moves so much more distance in the same time. The period of the wave form in the air is the same as the period of vibration of the bar, and therefore the mean velocity of the air particles is greater.

When the air wave delivers its varying pressure up to the liquid beyond the drum and the stapes, the mass and inertia of the liquid being greater than the air, the velocity of the liquid particles is again reduced, but the extreme range of motion of the liquid particles corresponds with the to and fro motion of the steel vibrator so far as period of time is concerned (making allowances for the time required by the wave form in the elastic air to travel to the ear).

The cochlea appears to be comparable to an engine which works by the pressure and rarefaction of air waves, and must be studied as we study an air or steam engine transmitting power through a piston to liquid in a vessel of constant volume.

Engineers will recognise in the case of a steam or air engine (disregarding losses due to abstraction of heat through expansion, etc.) that the units of power transmitted during any one small unit of the stroke is equal to the effective mean unit pressure multiplied by the area of the cylinder multiplied by the distance moved by the piston in unit time, or in other words is equal to the cubical displacement of the piston in unit time multiplied by the mean unit pressure.

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[1] Whether this would produce a sine curve or a distorted sine curve depends upon the nature of the various resistances, some of which, as in the case of viscosity, heat, and friction, may be affected in value by changes in velocity, but the position of the crests, hollows, and crossing points being maxima and minima, the time positions of the impulse points would not be affected, and it is to these maxima and minima that our attention is directed.

In the cochlea the same holds good, only that in the steam or air engine the motive power or pressure is regarded as uniform until the expansion is allowed to commence, and the pressure is then gradually reduced, whereas in the cochlea in a simple sound wave the pressure is in the central position of the stapes *nil*, then in phase I increased and subsequently decreased in pressure up to the end of the stroke, where the moving pressure is again *nil*. The pressure then increases again and subsequently decreases up to the central position, when it is again *nil* at the end of phase II (Plate V).

The rarefaction half of the wave form then enters and takes similar though reversed effect in phases III and IV, which are both negative, thus completing the cycle of change.

We have seen, p. 84, Plate V, that by the combined resistance of the tensor tympani and stapedius our nett effective pressure curve is changed in the wave form of the liquid.

Let us imagine the *effective mean* pressure of an indefinitely small portion of this altered liquid wave passing into the cochlea to be f per unit of area, and let s = space moved by the stapes (regarded as a piston) in the small unit of time during which the mean pressure is effective.

Then units of work or momentum transmitted to the liquid in unit of time $= f \times \text{area} \times s$,

and as area $\times\ s =$ *cu* displacement in unit time,

therefore $f \times$ *cu* displacement in unit time = unit momentum or units of work passed into liquid in unit time.

Further, as s or space moved in unit time = velocity, therefore $f \times$ area $\times$ velocity = work or momentum transmitted in unit time.

This is the formula used by engineers in estimating foot-pounds or units of work in an air or steam engine, with due allowance for friction and loss of heat.

As the total capacity of the cochlea is always the same, there being only one place of relief for displacement at the fenestra rotunda, the mass of liquid in motion is always the same, and therefore the pressure curve will also represent momentum.[1]

Assuming that change of momentum means an impulse, we should have an impulse in the stapes and the liquid moved by it, not only where pressure and velocity become *nil*, which is synchronous with the crossing points of the pressure air wave, but also at the crest of the wave where the acceleration of velocity and increase of pressure cease through the resistance of the ossicular muscles balancing the motion of the stapes in its extreme positions.

From the foregoing it will be seen that as *effective* mean unit pressure multiplied by cubical displacement represents units of power transmitted during any one small unit of time, the power transmitted at any moment is in proportion to the effective pressure. It is therefore the cubical displacement multiplied by the changing pressures which we must study in order to understand the action of the cochlea in transmitting not only impulses producing the sensation of pitch, but also the varying amplitudes of the sound wave representing varying units of power producing loudness and quality.

We have now to consider two other membranes in the cochlea, the basilar and Reissnerian membranes, which form a closed triangular space (canalis cochlearis) running spirally from the base to the apex of the cochlea and enclosing liquid endolymph which entirely fills the triangular spiral space and cannot mingle with the perilymph, a liquid of different chemical constitution which entirely fills the vestibular and tympanic passages. Any displacement of liquid occurring at the stapes can pass into the tympanic passage by the displacement of the Reissner and basilar membranes instead of going through the helicotrema, if the resistance is less through the former channel. Of course no particles of liquid pass the membranes, but the pressure causes displacement into the tympanic passage, and this displacement proceeds onwards to the fenestra rotunda, where it gets relief in the middle ear, which is normally at the atmospheric pressure.

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[1] Such a diagram is therefore comparable with the indicator diagram of pressures and displacements which is used in a steam or air engine to ascertain the useful units of work transmitted.

It will be presently explained that the basilar membrane on the vestibular side receives its intensified pressure of the liquid between the stapes and that membrane and that this excess pressure is diverted into the Corti arches and so carried out of the perilymph system to accomplish the external work of bending the auditory hairlets. This leaves the liquid in the tympanic passage at atmospheric pressure, just as in a hydraulic engine, when the piston rod carries the pressure out of the system to do external work, the exhaust water is lessened in pressure by the equivalent amount of effective pressure carried outside the system. The displacement of the exhaust water is the same, but the pressure is reduced.

The relative areas of the helicotrema and the basilar membrane (see p. 96) are respectively as 1 to 81, according to Dr. Keith's measurements, so that the liquid displacements will naturally select the shortest route and the line of least resistance to the fenestra rotunda, thus passing by way of the basilar membrane in preference to the helicotrema, the object of which aperture seems principally to be to form a liquid continuity between the vestibular and tympanic passage, securing equality in the distribution of fluid in these two passages.

The object of the reduction of area in the vestibular and tympanic passages, apart from the spreading out of the influence of the motion to an extended line of nerves to which I have already alluded, appears to be to reduce the mass of liquid moved. We have to deal with small forces, and the less the mass to be moved the less will be the resistance to motion. The total capacity of the perilymph liquid filling the vestibular and tympanic passages with that of the endolymph filling the scala media only amounts to 70 cubic mm. as measured by Dr. Keith. This represents a cube of liquid a little over 4 mm. measured on its side (about one-sixth of an inch). This is spread over a length of 35 mm., so that this attenuated mass is very minute.

At one time I thought the excitation of the nerves was due to the friction of the liquid moving in the tympanic passage underneath the basilar membrane. The difficulties I found in this explanation were, first, that any such excitation would increase as the velocities of the moving liquid approached the helicotrema, and that this would demand a different character of nerve for each velocity.

Secondly, that the nerves of hearing are all spread out in the organ of Corti in the scala media, and that there can be little or no longitudinal movement in the endolymph such as takes place with such vigour in the perilymph.

It was, however, evident that the basilar membrane must move up and down along with the motion of displacement in the endolymph, transverse in direction to that of the perilymph in the scalæ, and it was essential to investigate how the displacements of the endolymph and perilymph could be conveyed to the hairlets moving on the under surface of the tectoria, which physiologists recognise as the final point at which molar motion is converted into molecular motion or nerve current.

Between the vestibular and tympanic passages we have two flexible membranes, the basilar and the Reissnerian forming two sides of the triangular shaped scala media (cochlear canal), the liquid endolymph filling this space. These two membranes pass the displacements from one scala to the other, though no particles of fluid pass through either of the membranes. Thus the displacements of the fenestra ovalis, Reissnerian and basilar membranes, and the fenestra rotunda are equal, and the internal membranes move as though they formed part of the liquid.

We must now examine the passage of these cubical displacements of liquid through the basilar membrane.

Dr. Keith has measured the areas of the different membranes, which are as follows :—

Foot-plate of Stapes.

Fenestra ovalis ..	3 sq. mm.
or if effectiveness of displacement be diminished one-half through hinge ..	1·5 sq. mm. effective area.

Basilar Membrane.—This membrane tapers uniformly, the narrow end commencing at the fenestræ of the cochlea and the widest extremity ending near the helicotrema, this being in the reverse direction to the taper of the two scalæ. Its length varies from 35 to 40 mm. mean measurement round the convex margin of the spiral, and its average breadth is 0·333 mm., so that its actual area is 13·3 sq. mm., or nine times the effective area of the fenestra ovalis (stapedial foot-plate).

The area of the helicotrema is 0·175 sq. mm., or one-ninth of the effective area of the fenestra ovalis.

Ratios of the areas are therefore as follows :—

Helicotrema.	Fenestra ovalis.	M. basilaris.
1	9	81

Dr. Keith considers that the mean movement of the stapes, making allowance for the hinge, does not exceed ·025 mm., which is much less than the amount estimated by Helmholtz (who regarded it as a piston). If as above 3 sq. mm. be taken as the area of the stapes, the effective cubical displacement will, according to Dr. Keith, be 3 × ·025 = ·075 cubic mm. as a maximum.

It is evident that, taking into consideration the relative areas of the basilar membrane and the helicotrema, the line of motion of the displacements will follow that of least resistance, or through the basilar membrane, especially in the case of such rapid displacements as we have in sound waves.

The maximum mean movement of the basilar membrane would be—

$$\frac{\text{cubic displacement of fenestra ovalis}}{\text{area of basilar membrane}}$$

$$= \frac{0{\cdot}075 \text{ cubic mm.}}{13{\cdot}3 \text{ sq. mm.}} = 0{\cdot}0056 \text{ mm.}$$

or approximately $\frac{1}{4500}$ inch,

this minute movement representing a *maximum* mean displacement when the basilar membrane is regarded as a series of pistons.

If there were no basilar membrane, but a rigid partition, all the displacement produced at the fenestra ovalis would have to pass the helicotrema, and the reduction of area would cause a considerable loss of pressure in the tympanic passage owing to fluid resistances. With a flexible basilar membrane the displacement is passed through to the tympanic passage, distributing itself along the gradually widening membrane towards the helicotrema.

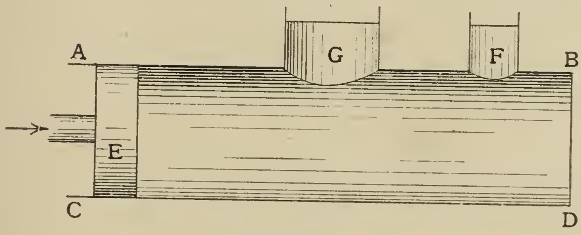

Fig. 36.

As liquid pressure in a closed vessel exerts itself equally in every direction, the unit pressure at any one moment which enters the cochlea is not affected by the shape of the vessel. If we imagine a cylinder, *A*, *B*, *C*, *D* (Fig. 36) closed at one end, *B D*, containing liquid of a certain unit pressure moved forward by a piston, *E*, and let two pipes, *F* and *G*, rise out of the cylinder, *G* being twice the area of *F*, on an increase of pressure due to the moving forward of the piston the liquid will rise in each pipe, *F* and *G*, the same height, and the increased height will represent the increased head of liquid or pressure, and the surface of the water in *F* and *G* will rise at the same velocity, but the displaced liquid will be twice the cubical contents in *G* to what it is in *F*. The same distribution would occur if there were more than two pipes to receive displacement; therefore the total displacement clearly divides itself in proportion to the respective areas through which it is passed.

The wide end of the basilar membrane comes close up to the helicotrema, so that, as already stated, probably little or nothing of the displacement passes that aperture.

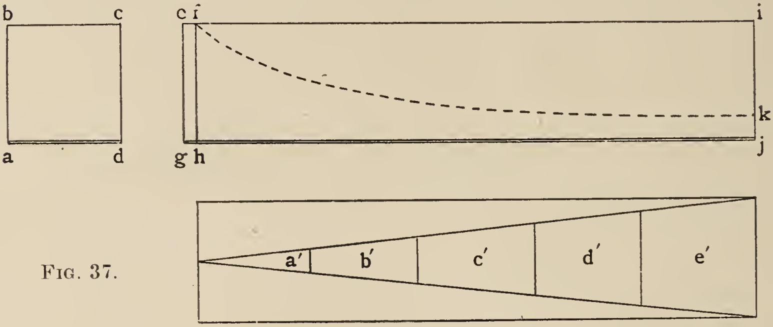

Fig. 37.

In the case of the cochlea we may assume that the vibrations of sound are so rapid that any passage of liquid through the helicotrema is negligible.

To simplify the problem of the action of the basilar membrane, let us suppose *a*, *b*, *c*, *d* (Fig. 37) to represent the end view of a long square box, *e*, *g*, *j*, *i*, with a bottom, *a d*, which can move as a piston vertically downwards; and let the length of the piston, *g j*, be five times the breadth of the box = 5 times *a d*.

Let another piston, *a b c d* move longitudinally through the distance *e f*, pressing liquid into the box, the cubical displacement of the liquid being *e f* × area of box $a\ b\ c\ d$. If the longitudinal piston, $g\ j$, be five times the length of $a\ d$, its area will be five times the area of the square piston, a, b, c, d; and as the cubical displacement of the two pistons must be the same, piston $a\ d$ must move down a distance one-fifth the distance $e\ f$.

Now imagine the piston $a\ d$, instead of being parallel, to be tapered, and make a plan view looking down on the bottom of the box and dividing the tapered piston into five pistons of equal length. The areas of each of these pistons, beginning at the left, will be in the proportion of 1, 3, 5, 7 and 9; each of these will take its proportion of displacement according to its area. The whole area will be $1 + 3 + 5 + 7 + 9 = 25$, and if the cubic displacement at $e\ f = 25$ cubic mm.,

a' in the tapered piston will take 1 cubic mm.
b' ,, ,, ,, ,, 3 ,, ,,
c' ,, ,, ,, ,, 5 ,, ,,
d' ,, ,, ,, ,, 7 ,, ,,
e' ,, ,, ,, ,, 9 ,, ,,

Total 25 ,, ,,

If a' equals an area of 1 square mm., it will in displacement of 1 cubic mm. move down a depth of 1 mm.

As b' equals an area of 3 square mm., it will in taking its displacement of 3 cubic mm. also move down 1 mm., and so on to e', when the area is 9 sq. mm., which, moving down 1 mm., displaces 9 sq. mm. × 1 mm. = 9 cubic mm.

For a small increment of displacement the space moved down in unit time or velocity of displacement through the tapered piston is therefore unity, but the *amount* of displacement is in proportion to the increasing areas. As the amount of displacement increases towards the far end of the box the liquid must, in order to supply the larger demand for displacement, move towards that end as the downward displacement of the long piston takes place. A cochlea would no doubt act on this principle, but the mass of liquid would be large if the passages were like the box in Fig. 37 of the same area.

The designer of this organ has reduced the mass by making the cochlea tapered in the opposite direction to the taper of the basilar membrane, as per dotted line *f k* (Fig. 37). This has the double effect of reducing the total mass of liquid in the cochlea and causing an increasingly rapid movement of the liquid towards the helicotrema, where the larger areas have to be supplied with liquid.

An inequality of area in the vestibular and tympanic passages will cause greater or less horizontal rapidity at the position of the inequality, but this does not affect the longitudinal displacement, which is still equal to the reduced or enlarged area multiplied by the velocity.

The effect of increasing velocity is that an additional resistance is set up which lowers the moving force or effective moving pressure at the stapes, thus flattening the wave form, which means reducing the amplitude of the motions.[1]

Inequalities in the passage of the cochlea such as described must therefore cause degrees of deafness by reduction of effective amplitude.

The real measure of the power conveyed to the senses is in the pressure and displacement of the liquid, and not in the pressure of the air wave, a portion of which is lost through liquid resistance and ceases to be a *moving* force.

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[1] As an illustration: If a pipe of uniform bore 20 ft. long will pass a gallon of water per second with a certain head or pressure, and the pipe be then constricted in area, at distances of, say, one foot apart, so that the water has twenty times in that pipe to be alternately increased and decreased in its velocity, the effect is to decrease largely the amount of water delivered per second, and the final pressure, because part of the pressure is taken up at each change of section in raising and lowering velocity in the inelastic liquid, and the amount of pressure thus lost reduces the *moving* force.

Now let us consider the change of displacement passed on towards the helicotrema in the vestibular and tympanic passages, still referring to drawing Fig. 37.

Up to end of a', 1/25th of the whole displacement passes through a' and 24/25ths go on past this point towards the helicotrema to supply areas b', c', d', e' in the basilar membrane.

Up to end of b', 4/25ths of the whole displacement pass through a' and b' and 21/25ths pass on towards the helicotrema.

To end of c', – 9/25ths pass through a', b', and c' and 16/25ths towards helicotrema.

To end of d', – 16/25ths pass through a', b', c', d' and 9/25ths forward.

To end of e', – 25/25ths, or the whole of the displacement, will have passed through the basilar membrane and nothing left to pass the helicotrema.

These displacements, it must be observed, are simultaneous in action.

If we now take the units of displacement which have to pass in the scala forward at end of each section a', b', c', d', e',

At end of	a'	we have	24	units
,,	b'	,,	21	,,
,,	c'	,,	16	,,
,,	d'	,,	9	,,
,,	e'	,,	0	

If the velocities to and from the helicotrema increased or decreased uniformly, which is the most favourable method so far as economy of power applied is concerned, the velocities in the scala would have to ascend in arithmetical progression 1, 2, 3, 4, 5,

$$\text{and as } \frac{\text{displacement}}{\text{velocity}} = \text{area},$$

the following table will show the successive areas to comply with this condition.

At end of	Unit velocity.	Unit displacement.	Area.		Area.
a'	1	24	$\frac{24}{1}$	=	24
b'	2	21	$\frac{21}{2}$	=	10·5
c'	3	16	$\frac{16}{3}$	=	5·33
d'	4	9	$\frac{9}{4}$	=	2·25
e'	5	0	No area required beyond this point.		

The aperture of the helicotrema exists, but no displacement passes.

If the whole of the displacement passed through the helicotrema and there were no basilar membrane, the displacement would be unity throughout the vestibular and tympanic passages, and the curve of sectional areas would be a rectangular hyperbola. See Fig. 38, p. 103.

This is obvious as area × velocity $= 1$

$$\text{therefore area} = \frac{1}{\text{velocity}}$$

At end of a area will be equal to $\frac{1}{1} = 1$
,, b ,, ,, $= \frac{1}{2}$
,, c ,, ,, $= \frac{1}{3}$
,, d ,, ,, $= \frac{1}{4}$
,, e ,, ,, $= \frac{1}{5}$

and a curve drawn through these ordinates will be a rectangular hyperbola.

On Fig. 38 I show in dotted lines this hyperbolic curve of sectional areas, the last ordinate at 5 representing the area of the helicotrema. The full line above represents the distortion of the areas caused by the total displacement being gradually passed through the increasing areas a', b', c', d', e' of the basilar membrane as in Fig. 37.

There are in all the various sections of the cochlea made by Dr. Keith the bell-mouth character as the sections approach the fenestræ and the sectional areas approximate to the curves described. It must, however, be remarked that slight deviations in calibration shown on the various sections (which deviations may be due to the extraordinary difficulty in measuring the areas in such a minute spiral tube, or that the samples dealt with had functional defects which an ideal cochlea might not show) do not affect the displacement, as velocity and area being always reciprocal adjust themselves and do not affect the proportion of displacement passing through the tapered basilar membrane at its different sections.

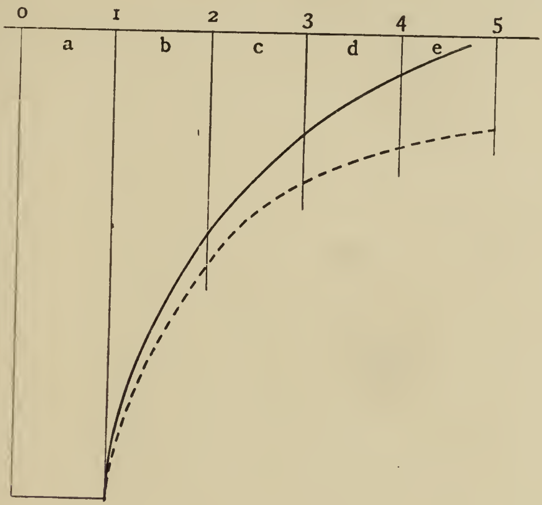

Fig. 38.

Let us now suppose that the effective nerves commence at the end of *a′* (Fig. 37) and that, say, 3,000 oblong pistons representing the Corti arches be placed between the end of *a′* and end of *e′* forming a series of 3,000 rectangular pistons varying in length according to their position in the tapered membrane.

Supposing that at end of *a′* (Fig. 37) the length of the piston was 1 and at the end next the helicotrema 5, then at the end of *b′* the length of piston would be 2; at *c′* 3; at *d′* 4; and at *e′* the length of piston would be 5.

There would be $\frac{3000}{4} = 750$ oblong pistons between each

division. That is, the area of first piston commencing at
end of a' would be 1
the next $1 + \frac{1}{750}$
,, ,, $1 + \frac{2}{750}$ and so on
at 2 $1 + \frac{750}{750}$ .. .. $= 2$
and so on between the other three divisions.

The last would commence at 4
the next $4 + \frac{1}{750}$
,, ,, $4 + \frac{2}{750}$ and so on to the last piston in
the cochlea close to the helicotrema
$4 + \frac{750}{750}$ .. .. $= 5$

Each piston would take its proportion of the total displacement, passing the motion, as will be presently shown, to the bent levers known as the Corti arches.

As each piston moves up and down with its neighbour the same distance, they may be (and are in nature) connected, and the whole membrane moves together.

One of the great difficulties encountered in the Helmholtz theory of resonance in the fibres of the basilar membrane is that these fibres are not free but connected sideways. In the displacement theory there is no difficulty presented by this side connection, as all parts of the basilar membrane rise and fall the same amount together.

We thus see that as the areas of the pistons increase towards the helicotrema in proportion to the displacements it is evident that the fraction $\frac{\text{displacement}}{\text{area}}$ will in each case be unity, so that all the pistons would move down the same vertical distance throughout this length of the cochlea, and if the unit of time were very small the amount moved down would represent the velocity of the piston.

As the total capacity of the cochlea is always the same, and, referring again to Fig. 37, as the amount of displacement required at each piston is in proportion to the areas 1, 3, 5, 7, 9, it follows that in order to supply liquid for this increasing amount of displacement towards the apex of the cochlea the velocity of the particles moving in the scalæ toward or from the wide end of the basilar membrane must be accelerated or retarded; hence the reduction of areas in the successive sections of the scalæ towards the helicotrema.

Each of these vertical cubical displacements passing the basilar pistons into the scala tympani moves in a direction at right angles to the direction of motion in the scala vestibuli and must find its shortest route to the fenestra rotunda, which is the only point of relief.

Throughout the whole length of the vestibular passage the horizontal displacement for a small increment of time is the constant;

$$\text{or displacement (1)} = \text{area} \times \text{velocity}$$

$$\text{or velocity} = \frac{\text{displacement (1)}}{\text{area}}.$$

When the motion turns at right angles and enters the rectangular pistons the velocity becomes the constant and

$$\text{velocity (1)} = \frac{\text{displacement}}{\text{area}}.$$

When the motion again turns at right angles back into the tympanic passage the displacement again becomes the constant and $\text{velocity} = \frac{\text{displacement (1)}}{\text{area}}$.

This velocity in the tympanic passage owing to the enlarging sections of the passage is diminished until it arrives at the fenestra rotunda, when it is practically the same as at the fenestra ovalis.

Thus every increment of velocity of the liquid at the stapes is reproduced as an increment of velocity in the vertical movement of the pistons of the basilar membrane, but reduced in range and therefore in velocity in the proportion of the total area of the basilar membrane to that of the fenestra ovalis, which is according to Dr. Keith's measurements as 9 to 1.[1]

We have now to consider the means by which the movements and velocities of the basilar membrane are conveyed to the hair cells.

The Corti arches are a series of bent levers about 3,000 in number (Fig. 39). The inner leg of each arch rests upon the relatively rigid limit of the internal spiral ligament; the outer leg upon the basilar membrane, which for convenience we will still regard as a series of pistons. Any up and down motions of the membrane therefore cause the arches to rock, describing an arc round the point of fixed support of the inner leg. The motion of the apex of the Corti arch will be similar to the motion of the membrane as it passes through the bent levers of the Corti arch. There is a membrane attached to this apex which is known as the membrana reticularis. This membrane stretches over the inner and outer cells like a wire net through the apertures of which the hair cells project. There are slender connections

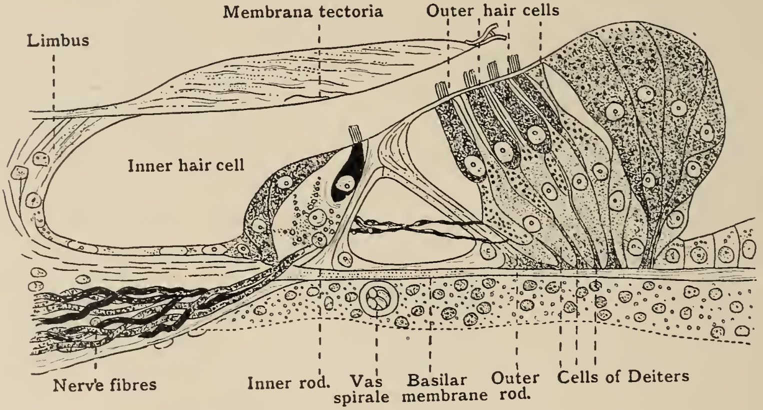

FIG. 39.—SECTION ACROSS THE ORGAN OF CORTI (RETZIUS). In this figure the tectorial membrane has been torn away from its normal attachments to the organ cf Corti.

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[1] It will be seen later that this proportion of 9 to 1 is ultimately increased to 4½ to 1 by the peculiar construction of the basilar membrane.

between the outer and inner margins of the tectoria and the reticular membrane internal to and external to the hair cells. These connections, which have been observed by several anatomists, no doubt prevent the tectorial membrane floating away from its contact with the hairlets.

Fig. 39 on a large scale (the form being taken from a section highly magnified of the middle turn of the human cochlea by G. Retzius—Quain's Anatomy) shows how the rocking motion will also cause movements in the ciliary processes of the hair cells. The ciliary movements affect the hair cells in such a way that with each definite motion of the cilia a nerve impulse is generated in the hair cells and transmitted by them to the fibres of the auditory nerves, the terminal ramifications of which reach or even penetrate the substance of the hair cells.

The membrana tectoria is described as resting on and receiving into its substance these hairlets or ciliary processes,[1] and as the reticular membrane supporting the foot of each hairlet moves to and fro driven by the movements of the basilar membrane through the Corti arches, we are justified in supposing that the flexure of the hairlets will produce stimuli of a tactile nature.

These minute motions due to successive increments of pressure in the air wave are thus delivered to the organ of Corti and tectorial membrane.

As the air wave form advances into the cochlea the increments of pressure in a small unit of time vary according to the form of the wave and the resistance of the ossicular muscles, and this form of the total wave in the liquid of the cochlea is reproduced in the vertical motion of the basilar membrane at each section and carried on by the bent levers of the Corti arches to the tectorial membrane, all the levers moving simultaneously and having the same range of motion through the whole length of the basilar membrane.

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[1] In Fig. 39 the tectorial membrane is represented as torn off the surface of the organ.

Having shown that the top of the basilar membrane regarded as a piston has a motion similar to the stapes, I must now point out that the actual form of the displacement is not rectangular, as it would be if regarded as a piston, but takes the form of two triangles in section (Fig. 40). The breadth of the basilar membrane is divided into two distinct parts—the elastic arcuate zone, *a e*, forming the base of the Corti arch, and the pectinate zone, *e d*, which is inelastic and to some extent rigid, which runs from the foot of the outer rod of the Corti arch to the internal spiral ligament at *d*, on which it hinges, in the falling and rising of the membrane. The outer foot of the Corti arch rests not in the middle of the membrane, but about halfway between the centre and the pivot of the Corti arch at *a* (Fig. 41).

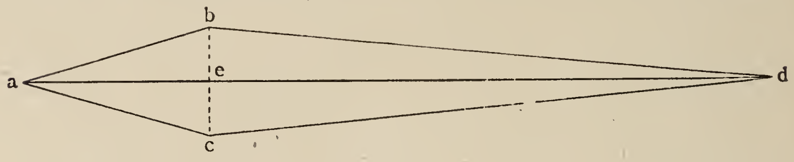

Fig. 40.

Dr. Keith has pointed out to me that at the attachment of the rigid pectinate zone to the spiral ligament at point *d* there is a series of radiating ligaments which spring from the sides of the vestibular and tympanic passages, and which form a securely braced anchorage for the support of the end of the pectinate zone, which can thus move as a hinge at *d* when the other end moves from *c* to *b*.

We may regard the movement from *c* to *b* as a straight line, as the length of the chord is so minute compared with the length of the rod *e d*.

The Corti arch, *a f e*, Fig. 41, rises and falls on the hinge at *a*, and as the point *e* is assumed to rise in a vertical straight line to *b*, there must be a slight angular change at *f*, as the subarcuate zone, *a e*, stretches in passing to *a b*. Although it is difficult to detect an actual hinge at this point, yet there is a cleft in the junction of *a f* with *e f* at the point *f* which appears to enable a certain minute amount of flexure to take place in the movement of the arch.

It is evident that the stretch of the arcuate zone will be the difference between length *e a* and *b a*, and again below the difference between *e a* and *c a*.

If we now postulate an initial tension existing in the whole breadth of the membrane from *a* to *d*, the same tension passing through both zones when the membrane is in the central position and pulling at the anchorages *a* and *d*, we recognise a duplication of the action of the tensor tympani and stapedius muscles.

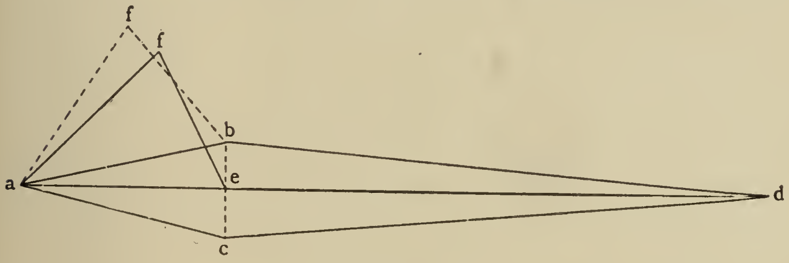

FIG. 41.

On p. 39 I have described the delicate balance obtainable in the motion of a point in the centre of an elastic band with an initial stretch over its whole length.

Suppose that, instead of a horizontal band elastic in its whole length, we divide its length into two parts, *a e*, with elastic properties, and *e d*, inelastic.

Then if an initial tension is put upon the whole length *a d*, which tension passes through both the inelastic and the elastic portions of the membrane, we shall find that in putting pressure downwards or upwards at point *e* the same delicacy of balance will be obtained in the vertical direction as we found in the horizontal, and that delicacy will be at its maximum when *e* is in a straight line between *a* and *d*. The slightest pressure up or down on *e* will further stretch the already initially stretched elastic zone, and directly the vertical pressure is taken off the membrane will return to its central position in consequence of the initial tension in the whole membrane augmented by the increased tension due to the vertical motion of the point *e* on the line *c e b*.

As in the case of the combined resistance of the ossicular muscles (p. 40), this resistance is reversed in direction as the stapes passes the central position, so in the basilar membrane the resistance of the elastic zone is reversed in its direction as point *e* passes its central position. Whatever distributed pressure over the whole membrane deflects point *e* either up or down, the opposing resistances of the tensions tend to pull the membrane back towards the central position as soon as the distributed pressure is removed or lessened.

If we now follow the comparison through the different phases of the wave form,

Phase I, Plate V, in the movement of the stapes corresponds with the motion of the basilar membrane from the central position *a e d* down to position *a c d* (Fig. 41).

In moving this distance the resistance of the initial tension between *a* and *d* is increased by the lengthening of *a e*, the elastic subarcuate zone, to *a c*.

The displacement of the liquid drives the point *c* down, and as there is no downward movement at *a* and *d* the whole moving pressure is concentrated on point *c*, from which the power is transmitted to the resistance of the bending hairlets through the Corti arches.

The point *c* corresponds with point *F* (Plate V), which also corresponds with the crest of the compression part of the air wave, and the point *c* cannot move further for the same reason that the stapes could not move further than *F* in Plate V, the pressure being at a maximum, and the resistance of the ossicular muscles in the case of the stapes, the elastic resistance of the subarcuate zone in the case of the basilar membrane added to the resistance of the bending hairlets balance the forward pressure of the liquid, so that there is atmospheric pressure at *c* both above and below the membrane and motion therefore ceases.

In phase II *c* is ascending to *e* (Fig. 41), this motion corresponding to phase II in the stapes movement. Here the potential energy in the tension on the subarcuate zone exerts itself, following the lessening pressure of the liquid above the membrane until it arrives at the central position, *e*, following the motion of the stapes.

In phase III the rarefaction part of the air wave commences to take effect. The stapes moves to its extreme outward position marked G^1 (Plate V), corresponding with the maximum rarefaction of the air wave, while in the basilar the apex of the membrane arrives at *b*, the subarcuate zone being stretched between *a* and *b* (Fig. 41).

In phase IV the potential energy in the subarcuate zone and the initial tension through both zones pull the membrane back to the central position against the changing negative pressure above the membrane.

The movement of the stapes and the basilar membrane must be synchronous, because the incompressible liquid is driven forward at the same successive pressures due to each time increment from the stapes to the basilar membrane, both displacing the same amount of liquid in each increment of time and therefore causing a similar motion though reduced in range in inverse proportion to the relative areas of the stapes and the basilar membrane.[1]

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[1] The pressure is divided over the whole breadth of the membrane. It is *nil* at the central position, *e* (Fig. 41), and also *nil* at the position *b* and *c*, so that at these positions the lines of the displacement triangles will be straight.

If any bending could take place it would be at the position of maximum effective pressure, which is halfway between *b* and *e*, also between *e* and *c*, but this will not affect total displacement, and whatever the pressure of

From geometrical considerations it is obvious that the total height of the two triangular displacements from upper to lower apex must be twice the height of an equal rectangular displacement.

In the rising and falling of the outer leg of the Corti arch let a, b, c, d (Fig. 42) represent equidistant vertical spaces through which its attachment with the membrane rises and falls over one-quarter wave-length.

The outer foot of the Corti arch at a, in moving through its vertical travel of one-quarter wave-length, passes through equal spaces ab, bc, cd, causing successive displacements.

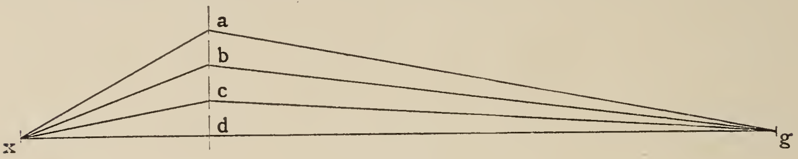

FIG. 42.

At b, a displacement of triangular areas $abx + abg$
,, c, ,, ,, ,, $acx + acg$
,, d, ,, ,, ,, $adx + adg$

and similar symmetrical displacements on the other side of the base line representing the adjacent quarter of the wave-length.

The vertical heights, ab, bc, cd, are each double what they would have been in a rectangular displacement of the same capacity. Therefore not only each increment of vertical motion is doubled between a and d, but the whole travel from a to the corresponding position below line xg would be doubled. This would alter the relative motion of the apex of the membrane as compared with that of the stapes from 9 to 1 as a piston, to 9 to 2 as equivalent

displacement it must be always concentrated upon the moving line c, b, e, as there is no vertical motion at either a or d, so that the whole effective energy of displacement must pass through line c, e, b and be passed on to the levers of the Corti arch.

triangles, although the areas representing total displacement are the same. It is also obvious that the lineal movements *ab*, *ac*, and *ad* will be in proportion to the corresponding cubical displacements shown in the triangles.

The inner leg of the Corti arch rests at *x*, Fig. 43, upon the edge of the spiral lamina, which coincides with the inner support of the basilar membrane. This foot of the arch forms a pivot for the inner leg of the arch to move through a small angle. When the basilar membrane is in position *a*, the position of the inner leg is shown to be *x a′*; the length *a a′*, *g g′* and in all intermediate positions being constant, the motion of the apex of the arch from *a′* to *g′* will be similar to the vertical motion from *a* to *g*.

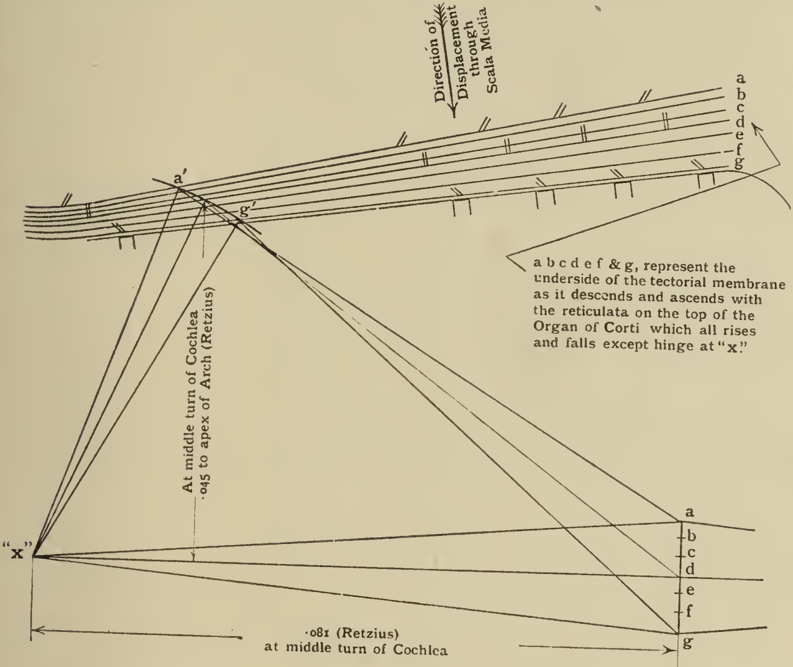
Direction of Displacement through Scala Media
a
b
c
d
e
f
g
a′
g′
a b c d e f & g, represent the underside of the tectorial membrane as it descends and ascends with the reticulata on the top of the Organ of Corti which all rises and falls except hinge at "x."
At middle turn of Cochlea ·045 to apex of Arch (Retzius)
"x"
a
b
c
d
e
f
g
·081 (Retzius) at middle turn of Cochlea

FIG. 43.

In passing the displacements of liquid through the scala media, the whole of the Corti arch and all its attachments, except the end x of the inner leg, rise and fall with the displacement, also the tectorial membrane which projects from its connection with the limbus of the spiral lamina at a fixed point behind and above the inner leg of the Corti arch.[1]

I have shown on Fig. 43, at the apex of the Corti organ, the positions which will be assumed by the membrana recticulata through which the hairlets pass as the successive positions of the basilar membrane *a*, *b*, *c*, *d*, *e*, *f*, *g* are taken.

Dr. Keith and other anatomists have detected a connection both between the inner and the outer margins of the tectorus to the organ of Corti, so that the gossamer-like tectoria will move up and down with the displacement of the liquid endolymph, and such motion will not interfere with the transverse motion of the reticular membrane. The tips of the hairlets will be in constant contact with the tectorial substance.

The group of hair cells to the inner side of the apex of the Corti arch, together with the four groups to the outer side of the apex, will, as they are set within the reticulated membrane, move transversely across the face of the tectorus which is anchored to the denticulated lamina, and the tactile resistance of the tectorus will bend the hairlets to the right as the apex moves to the left, and to the left as the apex moves to the right. When the motion of the reticular lamina, from which the hairlets project and take their movements, ceases, at the end and middle of its stroke, the flexure of each hairlet reverses, as shown in the upper part of the figure. We will return to this later.

It must be noticed that, the endolymph being an incompressible fluid in a closed vessel and with the Reissnerian and the basilar membranes enclosing it, the varying pressure upon it caused by the advance and retreat of the stapes in the perilymph causes a displacement exactly equal to that of the stapes.

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[1] Dr. Keith points out (p. 208) that this end of the tectorus acts like a spring set on the denticulate lamina. It will, therefore, in the rising and falling of the Corti arches and their attachments add another elastic resistance to the motion of the basilar membrane which will also follow Hooke's law.

This being a liquid transmission of displacement, there is perfect control of power and velocity, and the motion of the membranes will be in strict accordance with the conditions of displacement, pressure, velocity and area which govern the motion of an incompressible liquid in an enclosed space of uniform capacity.

To ascertain the actual to and fro motion of the hair cells we must take into account the angle at which the reticular surface of the organ of Corti in the human cochlea passes from the point *C* (see Fig. 44). This angle varies[1] considerably in the drawings of different anatomists. Helmholtz shows the line from the apex along the reticulata to be parallel with the basilar membrane, while Retzius shows an angle similar to that on line *C D* in Fig. 44, and which I have adopted.

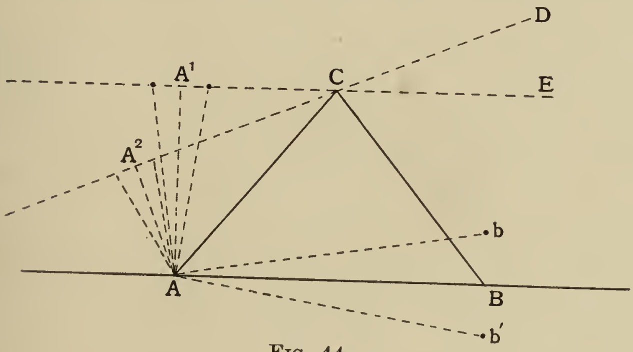

FIG. 44.

In the case of a small horizontal motion, the amount is measured by drawing a line, *A A*¹, through the pivot and at right angles to the horizontal direction, *C E*. The angular motion of the Corti arch at *B* will be the same as the angular motion at A^1, but the actual motion of A^1 will be :—

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[1] The angle also varies in different animals. Those with the most acute hearing have the most acute rising outward angle.—A. KEITH.

$$\frac{b\ b^1 \times A\ A^1}{A\ B},$$

the action being regarded as that of a bent lever $B\ A\ A^1$.

If we now raise the line of motion into position $A^2\ D$ (Retzius' position), and producing line $C\ D$ to A^2 drop a perpendicular line upon it through the pivot as at $A\ A^2$, the value of the motion of point A^2 in direction $A^2\ D$ compared with vertical motion at B is, according to the scale of Fig. 44, 1 : 2·3.

So that if $b\ b' = 0{\cdot}0056$ mm. (see p. 97), regarding basilar membrane as a piston, and twice that, or 0·0112 mm., if regarded as having equivalent triangular displacements (p. 112), the total motion forward of the reticular membrane along line $C\ D$ will be $\frac{0{\cdot}0112}{2{\cdot}3} = 0{\cdot}005$ mm., and the same backward, or 5 microns for a maximum displacement of 0·075 cubic mm. at the stapes, and the motions will be similar though reduced as compared with the motion of the apex of the basilar membrane in travelling on line $b\ b^1$, and therefore in proportion to the cubical displacements.

Helmholtz supposed that the hairlets were pushed upwards against the tectorial membrane, thus producing impulses.

There is a remarkable piece of evidence that the motion of the hairlet is transverse to the direction of the displacement through the basilar membrane to be found in the fact that the horizontal distance between the pivot of the Corti arch and foot of its outer rod where it rests on the basilar membrane becomes less and less as the membrane becomes narrower in its approach to the fenestræ. I have pointed out that the attachment of the outer rod to the membrane is at a point about one-fourth the breadth of the membrane from the pivot of the Corti arch. Now to have the same horizontal transverse motion at the apex of the Corti arch it would be necessary to increase or decrease the height of the apex of each Corti arch in direct proportion to the span of the arch.

Drawing No. 23, p. 235, in Dr. Keith's appendix shows the way in which the arches increase in span and height as they pass from the fenestræ, where the basilar membrane is narrowest, to the helicotrema, where it is the widest.

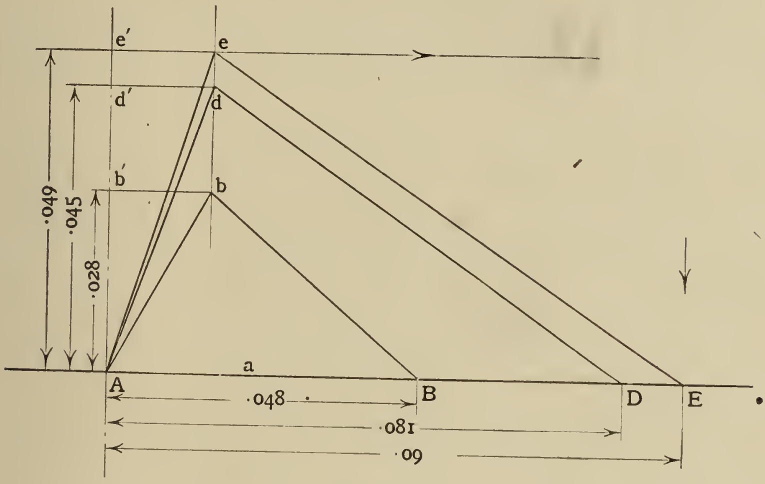

FIG. 45.

Retzius gives the height of the Corti arches and distance between attachment of the feet as follows (Quain's "Anatomy"). See diagram, Fig. 45.

Basal turn ..	$A\,B$ = 0·048 mm.	Ab' = 0·028 mm.	
Middle turn ..	$A\,D$ = 0·081 ,,	Ad' = 0·045 ,,	
Apical turn ..	$A\,E$ = 0·09 ,,	Ae' = 0·049 ,,	

Regarding the vertical movements of the points *E*, *D*, and *B* as acting on bent levers *E Ae′*, *D Ad′*, and *B Ab′*, and taking 0·0112 mm. as being the vertical motion of the outer foot of each Corti arch (see p. 116), the horizontal motions of the apices of the Corti arch will be as follows :—

At *b′* .. $0{\cdot}0112 \times \frac{0{\cdot}028}{0{\cdot}048} = 0{\cdot}0065$

At *d′* .. $0{\cdot}0112 \times \frac{0{\cdot}045}{0{\cdot}081} = 0{\cdot}0062$

At *e′* .. $0{\cdot}0112 \times \frac{0{\cdot}049}{0{\cdot}09} = 0{\cdot}0061$

These are the same to three places of decimals in millimetres, although the respective values of the leverages vary considerably.

This appears to suggest that the object of the Designer in raising the height of the Corti arches as the spans increase has been to maintain the same horizontal strokes at the apex of each arch, thus giving equal motion at each hairlet.

Nature thus gives us a strong hint as to the direction in which the action of the tectorial resistance takes place.

The reason for raising the angle of direction in the motion of the reticular membrane and hairlets is probably to make them lie at right angles to the direction of displacement of the endolymph as it passes from the centre of the Reissnerian membrane across the scala media to the centre of the basilar membrane.

The motion in the raised direction, as already pointed out, does not affect the similarity of the motion to that of the apex of the Corti arch, although it is reduced in range.

It has been already shown that the vertical motion of the basilar membrane is at its apex in proportion to the corresponding cubical displacements of liquid (p. 112), so that as this vertical motion is passed on to the tectorus we have a linear to and fro motion impressed on the reticular membrane which is exactly in proportion to the cubical displacements.

The displacement on the line of the movement of the stapes gives the different phases, thus (see Plate V, also Fig. 46):

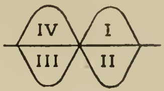

Fig. 46.

When these displacements pass through the basilar membrane they have turned at right angles and become thus (Fig. 47):

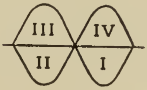

Fig. 47.

and when finally directed in the line of the reticulata they return again to the same order as the first, viz.:

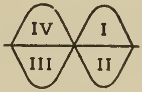

Fig. 48.

These changes are shown in their proper relative positions in Fig. 49, and the curves show the pressures in passing between the crossing points of the wave forms. At the position of rest corresponding with the central positions of the stapes, the basilar and the drum membranes, the hairlet will be upright with its upper end in the anchored tectorus, while its lower end moves to and fro, causing a bending of the hairlet, due to the resistance of the tectorus.

In phase I the movement to the right will cause the hairlet, *h*, to bend to the left, increasing in pressure in the centre, and then decreasing until the reticular membrane ceases to move forward.

In phase II, when the hairlet is in position h^1, the reticular membrane moves backward, first increasing and then diminishing in pressure until it arrives at the central position again, when movement ceases and the hairlet is again upright, as at *h*.

In phase III the rarefaction of the air wave form takes effect, and the hairlet is bent to the right, finally coming into position h^2.

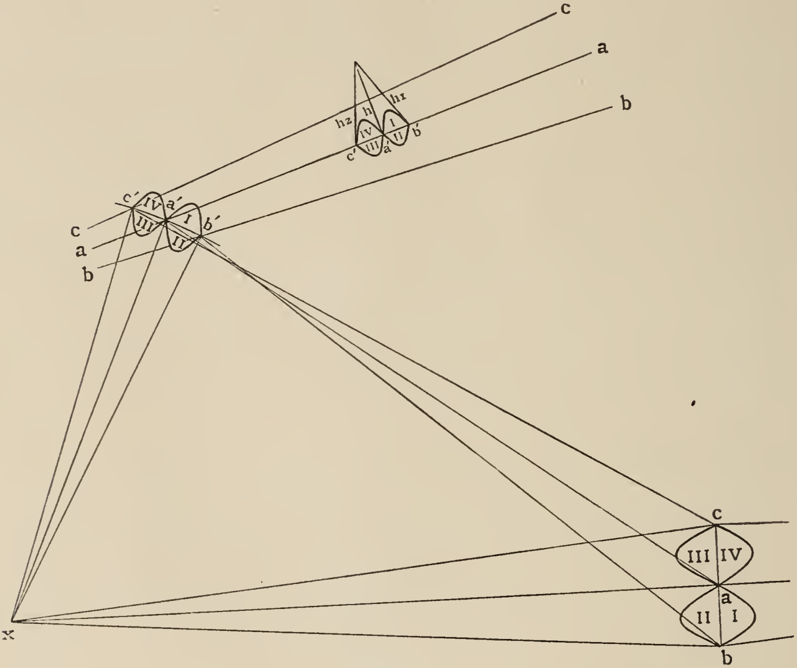

FIG. 49.

In phase IV the hairlet returns to its central upright position.

A simple illustration of the hairlet movement may be found if the back of a hair- or clothes-brush be regarded as the reticular membrane which is moved backwards and forwards to represent the motion of the foot of the hairlets. The hairs of the brush represent the auditory hairlets, and if with the left hand laid upon the tops of the brush hairs to represent the tectorus, the right hand is moved to and fro, the bending of the hairs is of the same character as that of the auditory hairlets.

Fig. 49 shows the way in which the different phases of the displacements are carried from the basilar to the reticular membrane, where the hairlets are bent as their motion is resisted by the tectorus holding their upper ends; only one hairlet is shown, but there are many thousands of them which all bend together, the change of flexure in each hairlet conveying to the brain an impulse at the moment motion begins or ceases. This cessation of moving pressure and momentum or cessation of units of work transmitted occurs when the basilar membrane, the stapes, and the drum membrane at the same moment take their central positions; also when the membranes have each arrived at their extreme positions—in other words, at the crests, hollows and crossing points of the air pressure wave as they arrive at the drum membrane.

The stapes and basilar membrane move together because connected by inelastic liquid, which controls completely their movements. The stapes and drum move together because connected by an articulated chain of ossicles. Thus the pressure of the air wave on the larger area of the drum is passed through the bent levers of the ossicles to the much smaller area of the stapes. This increases the unit pressure in the liquid of the labyrinth like a small intensifying press; the increase of pressures implying a corresponding decrease of displacement and motion and therefore of velocity. The drum membrane transmits its energy through the ossicles in a direct chain of bones, so that as the varying pressures of the air wave arrive at the drum they immediately meet the resistance of the inelastic liquids in the labyrinth and act upon the combined resistances of the tensor tympani and stapedius muscles; also on the elastic connections of the basilar membrane and other resistances (p. 138).

We have been considering up to this time the action of a so-called pure tone without harmonics, and have, I think, shown that the complete wave form in air is broken up into four half wave forms by the action of the resistance of the ossicular muscles and of the subarcuate zone of the basilar membrane.

We have now to consider the effect of a compound wave form passing into the liquid of the cochlea. In the appendix of my paper published in 1907 I give the diagram of a compound wave form of a musical perfect fifth produced by my compounding machine and which I reproduce in Fig. 50. In this, the upper diagram gives three simple air waves in the same period that the lower diagram gives two (2 : 3 being the ratio of vibration to produce a perfect fifth). In this case the vibrations have the same amplitude and with phases starting together.

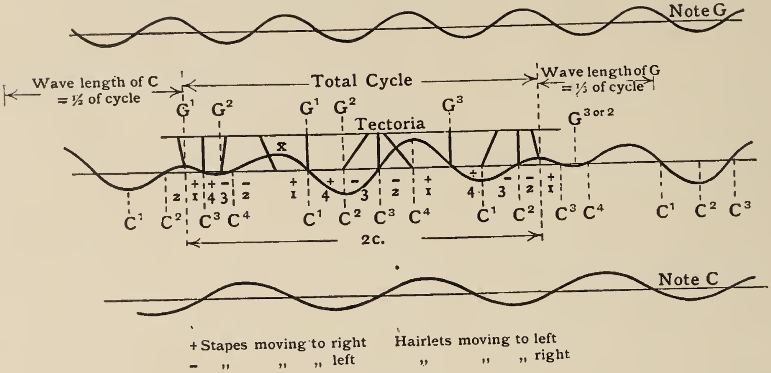

FIG. 50.

In the intermediate diagram is shown the compound wave form. This consists of a number of waves varying in amplitudes, the crests and hollows of which are modified in compounding from the original wave forms in the air. Each of these distorted wave forms successively passes into the cochlea through the stapes. According to Plate V, the stapes moves forward from the centre of its stroke as the front of the wave form enters, and retreats as the back of the compression wave form passes in. It continues to retreat while the front of the rarefaction wave enters and again comes forward as the back of the rarefaction enters and so on until the whole of the compounded wave has passed forward.

We have seen that through the action of the bent levers of the Corti arches the stapes and the reticular membrane move to and fro together, so that if we mark each phase of the compounded waves + or – according to whether the stapes and reticular membrane are moving forward or backward, we shall find that in the plus or forward motion the point of the hairlet will be held from behind, bending the hairlet over to the left, and when in the minus or backward movement the point of the hairlet will be held in front and the bending of the hairlet will be to the right.

The amount of bend in the elastic hairlet will be the measure of the pressure forward or backward of the wave every moment it is passing. This is in accordance with Hooke's law of elasticity. When there is no pressure forward or backward, which is the case at every crossing point of the compound wave form, the hairlet becomes upright, and contrary flexure commences immediately positive or negative pressure begins to exert itself.

If we now insert full lines to represent the angles to which the hairlets would bend as the wave passes in, we shall find a small flexure to the left at the right-hand end of the cycle as shown, on account of the resistance of the relatively stationary tectorus against the motion towards the right of the reticular membrane which is moving the lower end of the hairlet forward. This is only a slight bending, because the amplitude of this curve at that point indicates that the pressure and the movement of the stapes are both small.

Phase II of the motion then commences, in which the reticular membrane is moving backwards owing to the lessening pressure at the back of the wave form and the pull of the ossicular muscles. This relief of pressure brings the hairlet again upright as at C^2. Rarefaction then sets in, and the motion of the reticular membrane and the stapes is still backwards, but increasing in rarefaction. The hairlet is gradually bent to the right, the varying pressure from the tectorus on the point of the hairlet causing an angular displacement in proportion to the effective amplitude and pressure of the wave at each moment of time. At C^1, the hairlet has arrived at its extreme range of angular displacement, which corresponds with the extreme outward position of the stapes where the ossicular resistance balances the backward motion of the stapes. Contrary flexure then sets in.

As the back of the rarefaction part of the wave (phase IV) passes to the stapes, at the point G^3 the hairlet is again vertical. Contrary flexure then sets in as the front of the wave of highest amplitude in this cycle advances, and its forward advance causes the hairlet to bend its maximum amount to the left and so on until the complete compound wave cycle has acted upon the stapes and reticular membrane.

We have thus a contrary flexure taking place in the hairlet at every crest, hollow, and crossing point of the compound wave form in air. In every one of these positions momentum or work done has ceased and again commenced, and therefore an impulse is created; at the crests and hollows because the resistance of the ossicular muscles and basilar membrane balance the forward or backward pressure, and at the crossing points because pressure and velocity have ceased. The mass of liquid moved being always the same, the curves represent in their changing ordinates not only pressure but also momentum, or units of work being transmitted.

A change of momentum is also going on at every increment or decrement of pressure between these larger changes of flexure, but they are of a much less decided character. They influence the bending motion of the hairlet between the larger changes exactly in proportion to the effective pressures reproduced by the successive ordinates in the wave form. These minute changes of momentum in the constant mass of liquid in the cochlea will no doubt produce impulses, but of such a minute gradation that they would not cause so marked a stimulus such as we find in those attributable to the entire suspension of all momentum at the crossing points, crests, and hollows of the wave form. These minute changes of momentum appeal to our sensations as quality or timbre of tone, and their direct effect on the hairlet is measured by angular changes of the hairlets as they move between their extreme positions.

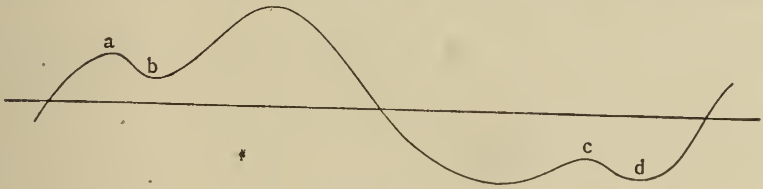

Fig. 51.

I have only taken one compound diagram, that of the perfect fifth, to illustrate this theory of analysis, but an examination of my numerous diagrams of many compounds in various phases and differences of amplitude show that the same reasoning applies to all.

Inmany compound wave forms, in addition to the gradual change of pressure between the crossing points and crests, we find subsidiary changes between the principal maxima and minima as at *a*, *b*, *c*, *d* in Fig. 51.

These cause intermediate changes of flexure in the hairlets as the points *a*, *b*, *c*, *d* pass in.

What we really come to in the displacement theory is that it is only the complete simple vibration of a pure tone which will be conveyed to the tectorus and cause a 4-phase vibration which bends each hairlet symmetrically. When compound waves enter, they each independently act on the same hairlet, so that, although we may have the compound vibration of many tuning forks travelling through the air at the same time, the method of the transmission of the compound motion by displacement enables each hairlet to move in bending, in sympathy not with one tuning fork but with all the tuning forks.

As the *total* pressure for each increment of the wave form in the cochlea increases in proportion to the areas towards the widening end of the basilar membrane, the power for each increment of the wave transmitted through the Corti arches must also be increased as we ascend the cochlea from the base to the apex.

Dr. Keith states in his appendix that towards the apex the cells and hairlets are increased in number, and I observe that in Quain's "Anatomy" (p. 328) Pritchard is quoted: "In most animals there are three series of outer hair cells, but in man there are four series except in the lowermost turn, and even five and six in the upper turns of the cochlea," and in p. 321, Fig. 269, of the same work he shows three outer cells only at a section across the *basal* turn of the human cochlea.

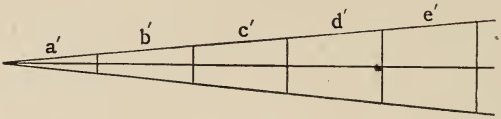

Fig. 52.

This increase in the number of cells and hairlets leads one to think that the increase in power transmitted from the wider end of the basilar membrane calls for a greater number of cells and hairlets to assimilate the increased power, and that from this point of view the upper turns of the cochlea are more important to audition than the lower so far as loudness is concerned.

A low power transmitted from the section *a*′ (Fig. 52) of the basilar membrane may not be able to move the hairlets in connection with that section, and even not in the case of *b′* section, and yet in the remaining sections, the power having so much increased, movement might be effected.

According to this view, in the dying out of a sound wave extinction of the excitement would take place first at *a′* section and move on until it disappeared entirely at *e′*. Pitch would also disappear in the same order, because the two sensations are concomitant effects.

It should be remembered that the maximum of the reticular movement is extremely small according to calculation (p. 116), only 5 microns, and the hairlet would therefore bend through a very small angle, but which in all its positions of angularity would represent the force resisted, in accordance with Hooke's law.

How that bending force is converted into equivalent nerve force is not a part of this inquiry.

CHAPTER IV

RESONANCE

Dr. Keith has pointed out in the appendix the difficulties anatomists find in adopting Helmholtz's view with regard to the sympathetic vibration in the cochlea being produced by resonance.

There are other physical difficulties which I will endeavour to point out.

The phenomenon of resonance arises from the elasticity of not only the vibrator and the resonator, but also from the elastic nature of the medium through which the sound wave travels between them.

This medium is the air. The to and fro motions of the membrana tympani are carried through the medium of the ossicles to the stapes. These bony levers form a chain transmitting a similar molar motion to the stapes as that produced on the drum by the successive condensations and rarefactions of the air wave entering the ear.

To put in motion the auditory hairlets which are suspended in the liquid endolymph of the scala media, the motions of the stapes must be passed through two independent liquids, viz., the perilymph, which fills both the scala vestibuli and scala tympani, and the endolymph, filling the scala media.

These are inelastic fluids contained in a closed vessel of constant volume, the particles of the liquid which are mobile being able to adapt themselves to the form the vessel may take when undergoing distortion as the pressure of an air wave acts on the external envelope of the cochlea. No motion would take place in the liquid but for the fact that when the vessel is squeezed by the pressure of the wave form arriving at the external surface of the cochlea (principally, though not exclusively, at the stapes) there is an exit for relief of displacement at the fenestra rotunda which allows this limp membrane to move outwards and inwards, but without altering the total capacity of the cochlea, which is always filled with a constant volume of fluid.

Let *A* (Fig. 53) be a steel bar fixed at the bottom and set in vibration to produce a simple tone without harmonics. The pulsations of air travel in every direction outwards, and come to a similar bar, *B*, which, through resonance, is put into similar vibration.

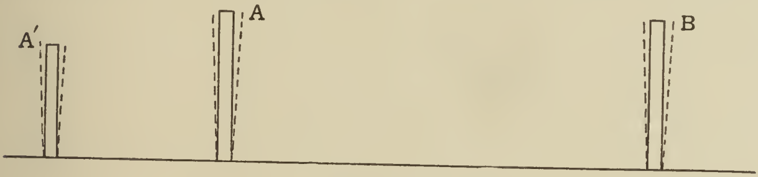

Fig. 53.

The note of *B* rises in intensity as the impulses from *A* accumulate, and then dies away as the vibration of *A* ceases or diminishes.

Now place another shorter bar *A′* near *A*, and put it also in vibration, and let this bar produce a note which is inharmonious with the bar *A*, that is *A′* and *A* have no harmonics in common; these two bars will send out different waves of sound which are compounded in the air and reach *B* together, but *B* will not produce two notes. It can only as a resonator produce one, viz., that of *A*. The other *A′* set of vibrations would only bring the rod *B* sooner to rest by damping periodically the natural resonance of *B* with *A*.

There is no doubt something simple, and to some minds fascinating, in the idea of the action of resonance to account for a sympathetic impulse in the auditory nerves, but it breaks down if one of the chief factors, viz., the elasticity of the liquid medium between the stapes and the auditory nerves, does not at these minute pressures exist.

In resonance where the medium between the vibrator and resonator is the elastic air, the wave form travels forward at the velocity of sound, and a certain time elapses before *B* imitates the motion of *A*, dependent upon the distance between the bars. Helmholtz, in his "Mechanism of the Ossicles," a book written after his Tonempfindungen, states with regard to liquid movement in the cochlea that "the communication of action through the whole mass is practically instantaneous and the labyrinth water under the influence of the sound waves moves virtually as a fluid absolutely incompressible would move under the same relation."

Again in resonance the resonator moves with the vibrator (making allowance for the time the wave in air takes to travel between the two) and the resonator requires a certain number of wave forms to influence it before it can accumulate its full amplitude.

In the theory propounded, the pressure at the middle of the stroke of the vibrating bar is at its maximum, whereas in the stapes at its minimum, and again at its minimum at the time position corresponding with the limits of the excursion of the vibrating bar. The motion of the stapes therefore does not in regard to pressure follow the motion of the vibrator as in true resonance.[1]

This being so, it seems difficult to identify resonance, which takes time to transmit its energy through air, with transmission through a liquid medium which is instantaneous.

Again, the motion of the stapes acting upon the liquid could only produce to and fro velocities equal to those of the stapes if the area of the cochlea beyond were uniform and the same as the stapes. This is not the case, as it varies very much in area as already pointed out.

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[1] This is very clearly shown on Plate VI at end of book.

There must therefore be some mechanical arrangement by which the movement of the stapes is restored before it reaches the nerve terminations. Again, as there is no connection between the endolymph, in which lie the hairlets of the nerve terminations, and the perilymph, which has an active longitudinal movement in the vestibular and tympanic passages, the only method by which motion can be transmitted to the Corti arches in the endolymph is by displacement. This can only be through the basilar membrane or Reissner's membrane. The latter is only a limp membrane apparently intended to act as a septum, preventing the mixing of the perilymph and endolymph.

The basilar membrane acts also in the same way, but, in addition, transmits motion to the bent levers of the Corti arches in their movements. I have already described the way in which I submit that this movement is carried on to the nerve terminations.

I have pointed out that in resonance (p. 129) one simple vibration of a bar will make another bar resonate only to the same tone. This was no doubt the reason why Helmholtz considered it necessary to have an enormous number of resonators which he sought for in the varying lengths of the fibres in the basilar membrane. He even then had to overlook the fact that all these fibres were united laterally, and therefore were not free to resonate without communicating vibration each to its neighbours throughout the whole length of the membrane.

If, instead of assuming resonance to convey the energy and the impulses of the wave form, we assume displacement of the liquid to act in the way I have endeavoured to describe, each hairlet would bend not as a pendulum, but with perfectly controlled movements which obliged the changes of flexure in the hairlets to correspond with impulses which I have shown by measurement to exist in the diagrams produced by the ohmograph illustrated in the earlier chapters of this treatise.

By this means each nerve terminal would transmit the same energy and impulses to the brain. With many thousands of these hairlets there would be some guarantee that functional failure of a portion of these would not seriously interfere with a transmission of energy which is divided amongst so many nerve terminations.

The theory also coincides with the latest view of physiologists with regard to the impulses of nerve excitations being coincident with the flexure of the hairlets protruding from the nerve cells.

Bone Conduction.

When the stapes is rendered immovable through disease, conduction is impaired but not destroyed. The vibrations of air are conveyed by the bones of the head to the outside envelope of the cochlea, and will cause movements of displacement in the liquid, provided the basilar membrane is free to allow the pressure to pass on to the hairlets, and that as motion of the basilar membrane takes place the fenestra rotunda is free to allow relief.

The vibrations of an open thin glass vessel containing liquid can be seen on the surface as converging waves, when the glass sides are made to vibrate. If that surface were closed so that no wavelets could be formed no motion of the liquid could take place, but if a flexible membrane were inserted in the side of the vessel motion would take place to and from the membrane.

If we imagine bone-conducted vibrations to be carried to the external surfaces both above and below the axis of the basilar membrane, the effect would be that the displacements caused from below would go direct to the fenestra rotunda without moving the basilar membrane, as there would be no stapes relief to take them ; those caused from above would pass through the basilar membrane and find their way to the fenestra rotunda, but without the intensifying effect produced through the drum and stapes. Hence the displacement of the basilar membrane and the motion transferred to the Corti arches would be much diminished, and hearing much impaired, but the character of the tone would remain the same.

I have pointed out that a duplication of the apparatus for producing the additional impulse in the crest of the wave is found in the peculiar triangular displacements of the basilar membrane and the elastic resistances of the arcuate zone. Hence waves which come by bone conduction without passing the mechanism of the ossicles and ossicular muscles will have the same distortion of wave form producing the additional impulse at the central position of the basilar membrane corresponding in time with that produced at the central position of the stapes when free to move. The resistance of the subarcuate zone of the basilar membrane due to its tension also limits the movement below and above as crest and trough of the wave form in air arrive, just as the tensor tympani and stapedius muscles act in the middle ear to limit the movement of the stapes.

I have pointed out on p. 114 that the movement of displacement of liquid carries the solids suspended to and fro with the motion of the liquid. The specific gravity of the solids in the cochlea being the same as that of the liquid, settlement will not be caused by gravity ; on the other hand, pressure in the liquid will have the effect of imparting a certain amount of rigidity to the solids in suspension and enable the skeletal framing of the organ of Corti to maintain its shape and carry out its functions, which it could not do if deprived of its liquid support.

The motions of liquid displacement are carried to the solids in suspension, and these will vibrate with the liquid in a way they could not do if suspended in air.

SUMMARY OF THEORY HERE PROPOUNDED.

The theory now propounded would enable a *pure tone* sounded by a tuning fork to travel through the route I have tried to describe and put in harmonic motion every hairlet imitating the vibrating movement at the source of sound.

In the case of compound tones the elastic air combines the effects of all the original vibrations of the pure tones forming the compound in accordance with Fourier's law. This compound wave travels along the air route until it arrives at the tympanum, where, through the delicately hung ossicles, the wave strikes upon the stapes behind which is the liquid contained in the cochlea. Every variation of pressure in the compound wave is impressed successively upon the mass of liquid throughout the whole cochlea. The only relief for the motion of displacement is at the fenestra rotunda, which moves to and fro simultaneously with the stapes. The displacement during any small unit of time multiplied by the effective pressure is the measure of the units of work or momentum transmitted to the liquid mass. The whole area of the pressure wave form (including both condensation and rarefaction) represents the cubical displacement multiplied by the average pressure, and is equal to the total units of work transmitted during the passage of the entire wave form. This is on the same principle as the efficiency of a steam or hydraulic engine is calculated from an indicator diagram. As the mass of the liquid in the cochlea is constant the *nett* pressure curve (that is, after allowing for the friction and other resistances of the liquid) represents the varying units of power transmitted for each unit of displacement. The exact determination of these pressures depends upon the resistances which would go to reduce the nett moving force, but the maxima and minima and crossing points of the compound wave would not be affected, and it is in these that we find the periodic impulses for which we search. Each hairlet under a compound wave moves to and fro in accordance with the displacements.

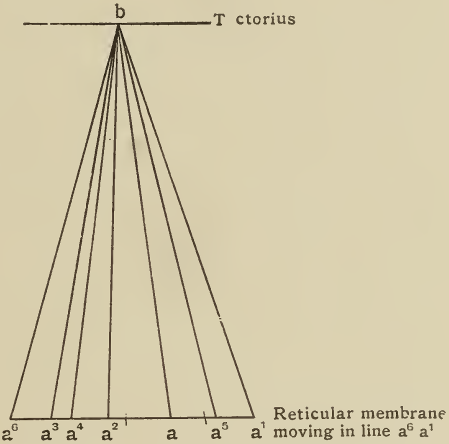

FIG. 54.

If the hairlet be represented by Fig. 54—the successive time positions may be: *a b*, $a\ {}^1b$, $a\ {}^2b$, $a\ {}^3b$, $a\ {}^4b$, $a\ {}^5b$, $a\ {}^6b$, etc., each contrary flexure of the hairlet at its support *a* creating an impulse. It would only be the simple pure tones which would give to the hairlet a pure symmetrical harmonic motion, but by the displacement of liquid under pressure every conceivable succession of bendings of the innumerable hairlets can be obtained to convey to the auditory nerve every impulse required to produce the pitch of each component and resultant tone.

These constitute the large changes of momentum. Apart from these there is throughout the whole of the effective wave form a much more gradual change of momentum, and these small changes also have in them impulses, but of such a minute character that they affect our sensations in a much less degree.

These extremely small changes of momentum each represent an increment or decrement of unit power passed into the cochlea ; and as the whole wave form is passed in, the cubic displacement is converted into a linear movement at the apex of the Corti arch ; this linear movement produces a tactile form of excitement on the tectorius, the resistance of which is again converted into the bending of the hairlets, the varying flexures of which convey to the brain the changes of momentum in a linear tactile excitement in proportion to the changes of momentum in the displacement of the liquid of the cochlea.

In a combination of tones, pitch and loudness are interdependent, and as the loudness disappears the sensation of pitch also disappears ; the vibrations of the basilar membrane having become so small that the hairlets receive no sensible movement sufficient to excite the nerve.

Any obstruction to the free movement of the liquids in the cochlea diminishes the effective mean amplitude of the wave form, and the units of power passed forward are reduced in proportion. Such obstruction would probably be one of the chief causes of deafness.

The accompanying diagram (Plate VI at end of book), which was suggested to me by Dr. Keith, shows the relationship between the impulses respectively at the air wave, the stapes, the basilar membrane, and the hairlet, as the air waves flow forward into the cochlea.

It will be noticed that in phase I the air wave at point *b* in advancing strikes the stapes in its central position, and as the air wave pressure rises in passing forward, the stapes is pushed forward into position *a*, which is a reversal of order, *b* being in front of *a* in the air wave, but behind in corresponding motion of the stapes.

In phase IV a similar reversal occurs ; in phases II and III this reversal does not take place. The arrows show that in phases I and IV the motion forward is in the same direction as the air wave, but in phases II and III opposite.

An attempt has been made to show the effect of the stapedius muscle in pulling outwards the stapes and that of the tensor tympanum pulling it inwards.

In phase I the attenuation of the line represents the action of the ossicular muscles pulling the stapes outwards, and opposing the greater pressure from the air-wave form.

In phase III the attenuation is on the opposite side of the stapes and is exercised in pulling it inwards.

In phases II and IV the tension is equal, and as an initial tension exists, the stapes always returns to the centre when no pressure is exerted by an air wave, either positive or negative.

As the impulse points are at the commencement and termination of each of the four phases, and therefore equidistant in point of time (in the wave form of a simple tone), this reversal cannot alter the periodic effect transmitted to the brain by those impulses. This would also apply to compounded wave forms in which, in one cycle, we have several systems. If we refer to p. 6 a disc syren is shown which has three or four systems of holes drilled near the periphery. If a blast of air be blown through a quill on such a series, it matters not in which direction, to right or left, the syren revolves the same combination of notes is heard, because the impulses for each of these series within the common cycle are still equidistant.[1]

NOTE. There is a reversal in vision in which the retina receives an inverted image, and which some action of the brain is supposed to correct. The analogy makes one think.

COMPARISON OF THE ACTION OF THE COCHLEA WITH THAT OF A HYDRAULIC ENGINE.

The scope of this paper is not intended to include any theory as to the final form which the transmitted energy takes at the tectorius in its passage to the brain.

Sufficient is not known as to the nature of the electric or other form of nerve transmission, nor of the physical action by which such current flows in the nerves, to justify speculative theory at this stage of inquiry.

However the units of power may behave on arrival at the tectorius, it appears clear that the form of tactile resistance generated must be of importance as being equivalent to the nett effective mechanical power transmitted by the air wave up to that point. If beyond that point molar motion continues we have at all events traced it so far.

If it is ultimately found that this transmitted mechanical pressure causes equivalent resistance in a flow of energy from a *different* source, passing to the brain through the tectorius and hairlets, such as we find in the case of microphonic action, we are still in the right path in studying the units of mechanical power arriving at the tectorius, as representing the varying resistances which would be required to impress upon the independent flow of energy proceeding to the brain similar energy and impulses as in the sound wave.

It has been shown that owing to the reduction of displacement in passing the pressure from the drum to the stapes the unit pressure in the cochlea is increased in inverse proportion to the respective displacements, and this augmented unit pressure acts upon the basilar membrane, putting a tension on the outer legs of the Corti arches and dragging them downwards. As the inner leg of the Corti arch turns on a hinge at point x (see schematic diagram 43, p. 113), the apex of the arch moves laterally, carrying with it the reticular membrane, and as it moves, the hairlets are bent to and fro by the resistance of the tectorius, the linear tactile pressures being, as already shown, in proportion to the time displacements taking place at the basilar membrane. As the reticular membrane moves forward the hairlets are bent backwards, and when the reticular membrane moves backwards the hairlets are bent forwards, the top of the hairlet being held by the tectorius. The reaction of the bending hairlets will be in the direction contrary to the motion of the apex of the Corti arch, and the potential energy of the hairlet in straightening itself will, reacting through the Corti arch, assist the ossicular muscles and the subarcuate zone of the basilar membrane in bringing the basilar membrane always to the central position as the crossing points *a*, *c*, and *e* arrive at the drum and stapes, at which moment atmospheric pressure prevails throughout the cochlea.

In a double acting hydraulic engine the piston is pressed forward by the high pressure liquid at the back of the piston and carries the pressure out of the cylinder through the piston rod to do external mechanical work.

In the cochlea the units of work are utilised in phases I and III in bending the hairlets and generating in them potential energy, a portion of which is delivered back to the basilar membrane through the very favourable angularities of the Corti levers during phases II and IV, thus assisting the potential energy in the elastic zone of the basilar membrane and the joint action of the tensor tympani and stapedius in bringing all the membranes back to their central positions.[1] The balance of the units of power represented in red lines in the power diagram, Plate V, goes to produce nerve current.

There would be no motion and therefore no work done but for the fact that the ordinates of the curve representing pressures are, *except at the crossing points, crests, and hollows,* always greater than the sum of the corresponding elastic time resistances of the ossicular muscles, the basilar membrane, and the hairlets, all of which act simultaneously in accordance with Hooke's law—modified from a space-pressure to a time-pressure basis.

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[1] The elastic resistance of the membrane of the f.o. will also tend to bring the stapes back to the central position. See note, p. 45.

The energy of each cycle of the four phases I, II, III and IV is impressed upon the liquids, producing, by displacement, pressures upon the tips of the auditory hairlets held by the tectorius, which pressures are in proportion to those of the effective air waves entering at the drum.

All the varying pressures in the rising and falling of the basilar membrane are carried through the endolymph space, which also rises and falls with the basilar membrane, but this does not interfere with the lateral motion of the reticular membrane, except that the whole Corti organ, including the endolymph space moving as on the hinge *X*, Fig. 43, is swayed up and down with the motion of displacement of the whole body of the two liquids.

Referring to schematic diagram, Fig. 55, when the crossing point of the air wave form arrives at the handle of the malleus there is atmospheric pressure throughout the cochlea, both in the air and liquid, and there being at that moment no moving pressure there is momentarily no motion.

As the air wave form passes in between positions *a* and *b* the handle of the malleus travels to the right and turns it round the ligamentous axis, *h*. As the head of the incus is articulated with the head of the malleus above the hinge, the head of both malleus and incus moves back in the opposite direction to the handle of the malleus, and the tip of the incus moves in the same direction as the drum membrane. As soon as point *b* in the air wave arrives we have completed phase I, and the handle of the malleus, also the stapes are in their right-hand extreme positions (dotted lines). The liquid in the space between the stapes and the basilar membrane being constant in volume causes exactly the same displacement at the basilar membrane, so that the dotted horizontal line shows the extreme lower position of that membrane ; the pressure of the wave form being balanced in these extreme positions by the resistances of the ossicular muscles, also of the subarcuate

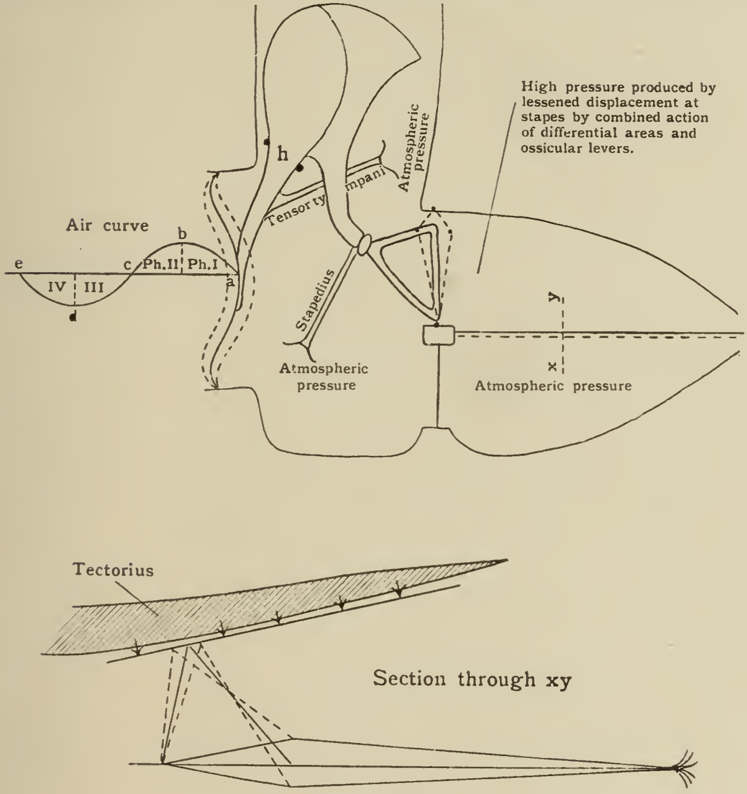

FIG. 55.

elastic zone of the basilar membrane, and by the reaction of the bending hairlets at the tectorial surface, all of which tend to pull the drum, the stapes, and the basilar membrane back into the central positions during phase II against the decreasing pressure as the air wave between *b* and *c* enters.

As soon as point *c* of the air wave arrives all the three membranes and the hairlets are in their central position again, and there is atmospheric pressure throughout the cochlea and therefore at that moment no motion.

Phase III now commences when *c* in the air wave arrives and rarefaction sets in. The motion of the handle of the malleus moves outwards to the left. This is caused by the atmospheric pressure from the middle ear pushing back the drum as the rarefaction part of the air wave between *c* and *d* advances; the pressure outside the drum being thus lowered, the atmospheric pressure inside is in excess and therefore pushes the drum membrane back outwards; at the same time the atmospheric pressure in the middle ear presses on the membrane of the fenestra rotunda, which action causes the liquid in the tympanic passage to follow up the motion of the basilar membrane and restore the displacement.

The action during phase IV is similar to that in phase II, only the pressure is negative instead of positive, and the resistances re-act in the opposite direction, not only in the resultant of the ossicular muscles but also in the basilar membrane, where in phase IV the resistance is pulling on the membrane to bring it down from above to its central position, instead of as in phase II, where it is pulling the membrane up from below. The reaction of the hairlets also assists this result.

It will thus be seen that at the beginning and end of each of the four phases a momentary cessation of pressure and therefore a cessation of movement take place. These are the moments when either there is no moving pressure or when pressure and resistances balance each other. The motion which takes place between these points is due to the fact that the pressure of each successive air wave creates its own reaction through the resistance of elastic solids which follow Hooke's law, in which force extending an elastic body causes a movement in space which is in direct proportion to the force exerted. The diagram of the air wave form is not a space-pressure but a time-pressure diagram, and an examination of Plate V shows that when the space-pressure diagram is converted into a time-pressure diagram during the period between the central and extreme positions of the membranes there is a difference in the ordinates of pressure which produce a double curve and generate the octave of the original tone owing to the subjective impulses brought into the cochlea, and which could not possibly be observed by resonators. The subjective effect also alters the character of the curve, which is no longer a sine curve.

In the case of the cochlea we have four membranes to consider :

(*a*) the drum membrane.
(*b*) the fenestra ovalis.
(*c*) the basilar membrane.
(*d*) the fenestra rotunda. See Fig. 56.

The basilar membrane is the true piston of the cochlea engine, as it is through the Corti arches attached to this piston that the units of power are carried out to the external work of bending the hairlets contained in the endolymph of the scala media.

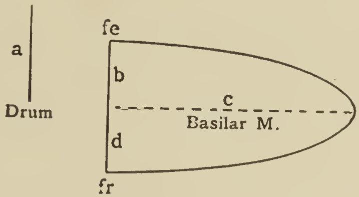

Fig. 56.

The increased pressure due to the intensifying effect of the reduction of displacement described (p. 48) is carried by membrane *b* (fenestra ovalis and stapes) into the space between *b* and *c* pressing down the basilar membrane which rocks each Corti arch and the reticular membrane attached to and fro, thus bending the numerous hairlets.

Let us now follow the action of the displacements. Membranes *a* and *b* are arranged in their movements as already explained (p. 48) so that a large *decrease* of cubic displacement takes place at *b* as compared with the displacement at *a*. This means a corresponding increase in unit pressure.

The displacement between membranes *b* and *c* is quite different, as there is no solid connection which can lessen or increase pressure. The liquid forms its own connection, adapting the velocities of its particles to suit changing areas, and therefore the displacement (which always equals velocity multiplied by area) remains the same, but the space the membrane *c* moves down in unit time (which equals in very small units of times the velocity) is less because the area *c* is greater than area *b*.

When the basilar membrane is in its central position the atmospheric pressure arriving from the middle ear through the fenestra rotunda is equal to the atmospheric pressure arriving from the middle ear through the fenestra ovalis. This tends to bring the basilar membrane into its central position, but this tendency is made much more active by the effect of the initial tension on this membrane which obliges it after displacement to come vigorously into this position of rest when the pressure wave is at the crossing point.

If we now suppose a wave form in the liquid to have a pressure at a certain moment of time of say $\frac{1}{1000}$th of an atmosphere, and that the pressure acts on the basilar membrane downwards from the central position (phase I), then at such time position of the compression part of the liquid wave form we shall have on the upper side of the basilar membrane a pressure of one atmosphere plus $\frac{1}{1000}$ atmosphere, and at the lower side one atmosphere. The difference, or $\frac{1}{1000}$ atmosphere will be the moving pressure *downwards*.

Similarly, at the same relative time position of the suction part of the wave form, on the under side of the basilar membrane we shall have one atmosphere and at the upper side one atmosphere minus $\frac{1}{1000}$ atmosphere. The difference or $\frac{1}{1000}$ of an atmosphere will be the moving pressure *upwards*.

The pressure downwards or the suction upwards, therefore, is $\frac{1}{1000}$ atmosphere, which is the pressure or suction above or below the axis of the liquid curve which was assumed.

Between the times of the crossing points of the liquid diagram of effective pressure in phases I and II the transmission of power is complete and requires no valve as in a hydraulic engine to commence and to terminate motion.

In a double acting hydraulic engine the fly-wheel has the surplus momentum transmitted to it which is restored again at the return stroke. In the cochlea the potential energy generated in the elastic resistances of the ossicular muscles, the basilar membrane, and the hairlets all acting together comes back into the system during phase II, and by the time that phase ends the whole of the effective residual units of work are passed on to the nerves.

The rarefaction part of the wave does its work in phases III and IV in the same way, only in this case due to the atmospheric pressure in the middle ear pressing the drum membrane back and through the differences of area between the drum and stapes intensifying the suction in the cochlea above the basilar membrane.

To put the matter in somewhat different words, the stapes moving from its central position to its extreme right inwards and then back to the central position forms a sub-cycle due to condensation.

The stapes moving from its central position to its extreme left outwards and then back to the central position forms a second sub-cycle due to rarefaction.

The two together form a complete cycle of action corresponding to the complete wave form.

Each sub-cycle is complete in itself and only passes forward to the auditory nerves the varying excess of units of work over units of resistance. These variations of excess all lie between the time positions of the crests, crossing points, and hollows of the air wave.

I have already explained that the intensifying arrangement (see p. 50) acts both ways, increasing pressure in the liquid above the basilar membrane, as well as increasing suction in the reverse action, so that the intensified pressure or suction is carried forward alternately to the hairlets through the Corti arch, and the pressure below the basilar membrane remains atmospheric.

The normal condition of pressure in the middle ear is atmospheric, and in order to prevent the external wave forms entering, the Eustachian tube is normally closed, but in case of barometic changes it is essential to adjust the external and internal pressures. The act of swallowing or yawning causes a slight opening in the Eustachian tube which restores the equilibrium. Any minute rise in the pressure due to the movement inwards of the drum membrane between the connection of the malleus and the periphery has no effect on the movement of the stapes, as such small increase of pressure is counteracted by the same pressure acting upon the fenestra rotunda which acts in opposition to the stapes.

The whole of the intensified moving action thus arrives at the hairlets from the upper side of the basilar membrane, and the liquid below always remains at atmospheric pressure.

The pressure of the wave form thus passes through the drum, the ossicles and the stapes direct to the liquid increasing the unit pressure in the cochlea.

In the suction part of the wave form the atmospheric pressure from the middle ear follows the drum membrane back as the rarefaction part of the air wave arriving lessens the external pressure; and the stapes is pressed back the same distance as it previously moved forward, this being due to the atmospheric pressure of the middle ear acting through the fenestra rotunda. As the drum and stapes are connected by the chain of ossicles the displacement at the stapes is increased by their leverages and the action due to the differential areas of the membranes, thus reversing the action which decreased displacement in the compression stroke.

This beautiful mechanical arrangement for raising the pressure in the vestibular passage of the cochlea without interfering with the transmission of the effective units of work to the nerves should provoke the admiration of the scientific engineer.

FURTHER EFFECTS PRODUCED ON THE WAVE FORM IN THE COCHLEA BY THE ADDITIONAL SUBJECTIVE OCTAVE GENERATED BY THE RESISTANCES OF THE OSSICULAR MUSCLES AND THE BASILAR MEMBRANE.

The octave produced subjectively in the mechanism of the ear, and which cannot be heard in any form of resonator, has an effect upon the differential tones which I think ought to clear up a long controversy as to their origin

In the discussion on a paper read at the Physical Society by W. B. Morton and Mary Daragh on February 15th, 1915, the late Professor Silvanus Thompson stated that the controversy was between Helmholtz and Koenig. Helmholtz contended that the differential tone had a vibration rate of $m - n$ when m was the higher and n the lower of the vibration rates of the two simple tones.

Koenig contended that he heard two differential tones, viz., $m - n$, also $2n - m$. I will take the actual figures given by Professor Silvanus Thompson.

If we have as primaries the notes of frequency 3328 and 2048 there will be heard according to Helmholtz the difference tones $3328 - 2048 = 1280$.

According to Koenig there will be heard not only Helmholtz's 1280, but also $2n - m$ or $4096 - 3328 = 768$.

Let us now look at the effect where an additional octave to each primary is produced subjectively.

In the cochlea we would receive four vibrations :—

m	3328
n	2048
$2m$	6656
$2n$	4096

Taking first the greatest frequency $2m = 6656$ we shall have the following tones and combinations :—

a	$2m-m = 6656-3328 = 3328$
b	$2m-2n = 6656-4096 = 2560$
c	$2m-n = 6656-2048 = 4608$
d	$m-n = 3328-2048 = 1280$
e	$2n-m = 4096-3328 = 768$
f	$2n-n = 4096-2048 = 2048$

a and *f* do not produce independent differentials, as the former is the same as *m* and the latter is the same as *n*.

The four independent differentials are : *b*, 2560, which is an octave above *d* ; *c*, 4608, which is the sixth harmonic above *e*, and therefore not very audible or helpful in assisting the perception of harmony ; *d*, 1280, which is accepted by both Helmholtz and Koenig ; *e*, 768, accepted by both Koenig and Professor Silvanus Thompson.

The simplest graphic method to show how these differential tones move is to further develop the diagram Fig. 1, described on p. 2.

This is shown on Fig. 57, in which 1, 1^1, 1^2, a full horizontal line, indicates the vibration rate of note *n* continuously sounding, while the full line, 1, 2^1, 3^2, indicates the higher note *m* continuously rising in pitch through an octave and a half, the vibrations at each musical interval being measured from the base line 0, 0^1, 0^2.

The first differential will run from 0 to $2^2 = m - n$ (*d*), accepted by both Helmholtz and Koenig.

The second differential will run from 0^1 to $1 = 2n - m$ (*e*), accepted by Koenig and Professor Silvanus Thompson.

In addition we also see in the graph the positions of
$2m - m$ (*a*) which is the same as m
$2m - 2n$ (*b*)
$2m - n$ (*c*)
and $2n - n$ (*f*) which coincides with n
and many others could be shown on the same principle.

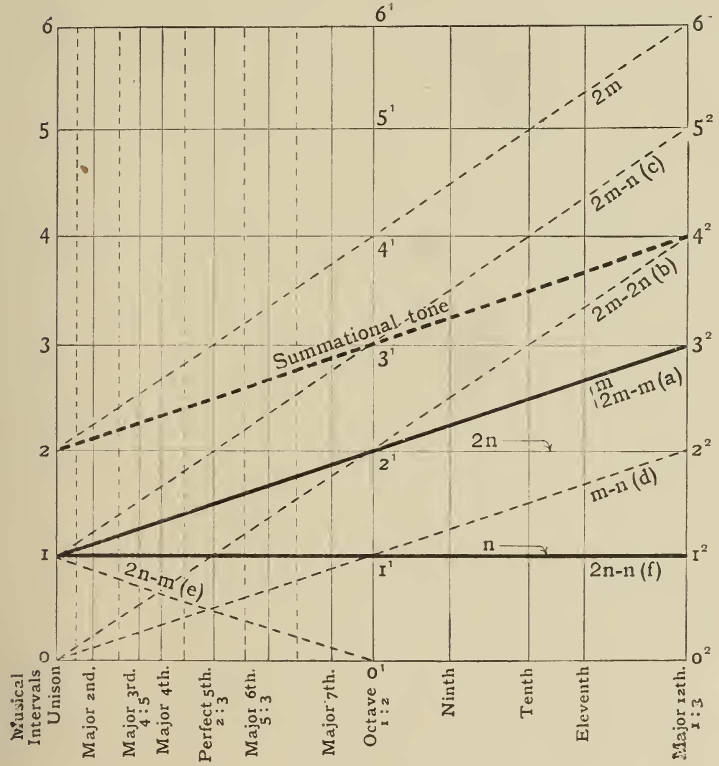

FIG. 57.

The *d* and *e* differentials are very distinctly heard in tuning the fifths of a violin, one rising and the other falling in pitch, and where they exactly coincide the violin strings are exactly in tune.

In the first and second chapters of this work I have shown that if two wave forms were compounded the crests, hollows, and crossing points in the compound indicated the time positions when impulses were required to produce the individual tones, also the differential and the summational tones.

We have followed the air wave form into the liquid of the cochlea and found that it becomes distorted through the resistances of the ossicular muscles dividing the original sine curve into two positive and two negative pressure curves which are no longer sine curves. The two positive curves, phases I and II, succeed each other above the axis, and the two negative curves, III and IV, succeed each other below the axis, so that if we lay these curves out in the order of their succession we shall find the appearance as shown on Plate VII, where two vibrations for note C are shown as a pure sine curve in air and immediately to the right the distorted pressure curve in the liquid of the cochlea.

In the upper figures of the same sheet are shown three vibrations for note G, a musical fifth above C, and contiguous to it the corresponding distorted series of curves in the cochlea.

Let us now combine these distorted pressure curves by plotting down the algebraical sums of their liquid pressures over a complete cycle.

The compound form in air and that in liquid are shown on the same sheet in the intermediate figures. A comparison of these two will show what a change has taken place in the wave form.

All the crests and troughs have become either crossing points or points of change in direction and pressure, while all the crossing points in the air wave still remain crossing points in the liquid. Additional crossing points have also come into existence.

The scale is too small to measure the relation between these impulses with those we require under this theory of harmony, but on Plate VIII I have plotted down to a more measurable scale the compound of two simple tones in the ratio of 3 to 5, or a musical major sixth.

In this compound the phases commence together and the vibrations are of equal amplitude.

The top diagram shows the sine curve in air, also the distorted curve in the liquid of the cochlea for the note A (musical notation). The lower gives the same particulars for the note C.

The middle diagram gives the curve in compounding the ordinates of the two distorted curves in the liquid. I have at the top of the sheet shown to scale the dimension of each wave-length in the original tones, also the wave-length of a summational tone, which, in the ratio of the vibration of C and A or 3 : 5, would be the total length of the cycle divided by 5 + 3 or one-eighth of the cycle. I have also shown the wave-lengths of the two first difference tones, viz. :—

Difference between 5 and 3 $(m-n) = 2$ in the cycle. Helmholtz.

Difference between 5 and twice 3 $(2n-m) = 1$ in the cycle. Koenig.

If with a pair of compasses the length of one complete air wave form by the scale, say C, is taken, it will be found that on the whole cycle a succession of intervals between crossing points corresponding to their dimension is revealed.

The same with length of A.

The differential notes when measured off also give all the recurrences required in the whole cycle to produce their effect, and the same with regard to the summational tones, which in this case are in two series, marked S and S′.

These recurrences need not always be in the same series, but may be in several series.[1] It is extraordinary to observe how the sinuosities of the complex compound curve adapt themselves to the requirements of the periodicity at the crossing points, crests, and hollows of the compound. I have marked one of the first differentials only on this compound diagram, but by applying the compasses it will be found that a number of such periodic impulses in different series occur throughout the cycle.

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[1] This is fully explained, pp. 7 and 8.

On Plate IX I have shown the same compound C and A, 3 : 5, but with different amplitudes, viz., 8 : 5, the larger amplitude being the lower note, C.

We see here a very different contour of wave form, but the same extraordinary adaptation of sinuosities to the time points required under the theory.

I have marked in this diagram six equidistant points in one series S as indicating impulses of summational tones.

3 points in a second series marked S^1
2 ,, ,, third ,, ,, S^2
2 ,, ,, fourth ,, ,, S^3
4 ,, ,, fifth ,, ,, S^4
2 ,, ,, sixth ,, ,, S^5
3 ,, ,, seventh ,, ,, S^6
3 ,, ,, eighth ,, ,, S^7
2 ,, ,, ninth ,, ,, S^8
2 ,, ,, tenth ,, ,, S^9
3 ,, ,, eleventh ,, ,, S^{10}

These form thirty-two impulses in the cycle in eleven series. I have not complicated the diagram with indications of the prime notes or those of the differential tones, but all these will be detected by the use of compasses adjusted to the wave-lengths of these various tones as given at the foot of the Plate.

It will be observed how accentuated every crest and trough of the air wave becomes as it passes into the liquid and as it comes under the influence of the elastic resistances of the ossicular muscles, the basilar membrane, and the hairlets. The unbalanced excess of pressure over these resistances causes the varying motions which produce the sensation of sound when carried to the brain.

With regard to the curve which produces these remarkable results. The ordinates of the full black curve (Plate V, Fig. 2) represent the sines of the varying angles through which the radius of the generating circle passes and are in proportion to the pressures exerted as the wave advances. The ordinates of the dotted black curve represent the versines of the same angles and are in proportion to the total elastic resistances, all generated by the sine wave pressures in accordance with Hooke's law of elastic solids, but adjusted to a time basis. The sine pressure wave whether positive or negative is always greater than the versine resistance except at 0°, 90°, 180° and 270°, which are four zero points.

The ordinates of the red curve will always be the difference between those of the sine curve and those of the dotted black or versine curve for each angle ; and in passing round the circle the signs of these will vary according to the conventions of trigonometry. The four phases will produce symmetrical curves in pairs alternately above and below the axis of the continuous wave form, and there will be four zero and four maxima points in each simple wave form, the latter being at 45°, 135°, 225° and 315°.

On p. 30 I have pointed out that I did not claim absolute mathematical accuracy in the identification of all the crests, troughs and crossing points of compounded sine waves with the periods of the principal tones, their differential and summational tones.

The late Sir Arthur Rücker and Dr. Alfred Western some years ago looked into the mathematical side of the question and informed me that these coincidences were not absolutely true, though nearly so, and perhaps sufficiently near to admit the theory.

The compound red curve which is not a sine curve appears to produce graphically a coincidence of these effects which is startling in accuracy, and subject to mathematical analysis this special curve would appear to possess properties which I first attributed, though with reservation as to accuracy, to the sine curve.

If this view be correct, we have in the cochlea an instrument which produces automatically a successive time register of the *effective* moving pressures positive or negative in the liquids of the cochlea which is analogous to the indicator diagram of a steam or hydraulic engine.

At the zero points and at the maxima of pressure and rarefaction there is a cessation of motion or acceleration in the whole mass of liquid in the cochlea causing a series of impulses which coincide not only with the periods of the original tones, but also, in numerous series, with the periods of the differential tones, the summational tones, and the harmonics, all contributing to the harmony of the combination.

From the foregoing it will be seen that while considering the pressures (positive or negative) generated in the liquid of the cochlea, as the constant succession of new air waves arrive at the ear, contemporaneous resistances are generated for each wave form at various parts of the cochlea, viz., 1st at the stapes, 2nd at the basilar membrane, 3rd at the hairlets, 4th at the stalk of the tectorius, and probably there may be other places. All these resistances are in proportion to the versine of the angle through which the radius of the generating circle is passing. Opposing and overcoming these we have the pressure of the wave form in the liquid which is in proportion to the sine of the same angle. At the beginning and end of each phase the pressures and combined resistances balance each other, but between these time positions there is a varying residual pressure the effect of which has to be accounted for. This residual pressure is represented by the red curve in Plate V, Fig. 2. It is unbelievable that these residual pressures act mechanically like bell wires upon the nerves to carry their message to the brain, but if it could be shown that an independent nerve current is always passing through the points where the hairlets press upon the tectorius, we should recognise in such an arrangement a microphone which would change the wave form in the liquid into a wave form of the nerve current in accordance with the great principle discovered by Professor Hughes. I am not regarding this postulate of an independent current as yet fit for acceptance. But I think that physiologists would do well to study the possibility of such a condition.

PREFATORY LETTER TO DR. A. KEITH'S APPENDIX ON THE ANATOMY OF THE INTERNAL EAR.

Royal College of Surgeons,
London, W.C.
16th February, 1917.

Dear Sir Thomas,

I have several reasons for asking you to allow me to add an Appendix to your work : the chief being this. It is a good many years now since you came to the London Hospital in search of details pertaining to the internal ear—that wonderful machine which transforms sound waves into brain messages—details which were not to be found in our text-books of anatomy. Yet some of those text-books on the ear are excellent—particularly Schäfer's volume on the special senses in Quain's "Anatomy" and Cannieu's contribution to Poirier's "Anatomy." Even these, however, have this defect : they treat the internal ear as if it were a piece of architecture and not a machine. Hence it is that anyone who seeks at present for a picture of the ear as a piece of working machinery has great difficulty in laying his hand on the exact facts he stands in need of. The searcher desires to see and examine the machine with all its parts set in working order and clearly visible to the eye. We have assembled the various parts of the machine and placed them, as we think, in working order, and we naturally wish that others may benefit by our labours. That is one reason for this Appendix.

It has not been an easy matter to verify all the structural details relating to the internal ear; it is an extraordinarily delicate and minute organ, and the thickness and hardness of the bone in which it is encased make access to it peculiarly difficult. We were fortunate in these earlier years to have the help of Mr. William Chesterman, who prepared at your cost three series of microscopical preparations of the human ear. All through our labours we have been verifying previous observations and making new ones. It seems therefore a pity if we did not place on record now the information relating to the internal ear—information which has cost time and toil to gather—that is another reason for my request.

Besides a representation of our anatomical facts will give those who are unacquainted with the anatomy of the internal ear an opportunity of testing the truth of your theory. The true and final test of any theory relating to any part of the animal body is its success in giving a complete and convincing explanation of the conformation and arrangement of its various parts. A clue to the structure of a machine lies in the discovery of the purpose for which it was designed and the manner in which its various parts are co-ordinated to secure that end. That is eminently true of the ear.

I am convinced that the theory you first put forward forty-one years ago, and which you have now succeeded in completing and proving, is the most convincing explanation which has yet been given of the manner in which sound waves are converted into brain messages. It is the most satisfying to the anatomist because it gives an explanation of why the parts within the cochlea are shaped and fixed in the manner known to him. It is certain to win the assent and support of physiologists, psychologists, physicists and musicians, because it explains phenomena of hearing which were inexplicable before. I can also see its utility to the clinician; he will find in it a basis on which he can account for certain obscure signs and symptoms. Perhaps I claim more for your theory than you yourself would be willing to admit.

In this Appendix I have sought to construct a working picture of the internal ear, by giving a brief historical introduction showing how our knowledge of that organ has grown up. I put together the organ of Corti, element by element, and inquire how each will be affected by displacing forces, such as arise from movements of the stapes. We cannot claim originality for our conception of the movements within the organ of Corti; others before us have recognised that the vertical displacements of the basilar membrane are transformed into transverse movements between the plateau of the organ of Corti and the overlying tectorial membrane. But what is new is (1) the discovery you published in 1876—that if a nerve-stimulus is produced at every "crest," "trough," and "crossing point" of any sound—however complex that sound might be—the brain will receive sufficient data to make possible a complete analysis of that sound. (2) Your demonstration that each complete sound vibration is made up of four phases and that each phase, acting against an elastic resistance, can give rise to a displacement stimulus. These are your patents.

As I show at the end of my Appendix, von Helmholtz's theory, although it has many critics, is still the most widely accepted theory of hearing. I could not express the attitude of our leading physiologists to von Helmholtz's theory or to any of its rivals better than has been done by Professor Starling in the last edition of his excellent "Principles of Human Physiology" (1915).

"This power of analysis must be due either to a battery of resonators in the end organs of the auditory nerve, or to the existence of a large number of nerve fibres, each of which is excited by a distinct number of vibrations per second, or, finally we must assume that the end organ of hearing is affected as a whole and that the nerve fibres transmit to the brain the different forms of waves caused by various complex sounds, the analysis being carried out by the cerebral cortex itself. This last hypothesis, the relegation of the powers of analysis to the cerebral cortex, is at the present time equivalent to giving up any attempt to explain the powers of analysis possessed by the organ of hearing."

And yet it is this last hypothesis, in spite of Professor Starling's criticism, that is advanced by you, and which has my whole-hearted support.

It is quite apparent, from the quotation just made, how widely the opinion is held that our power to analyse a complex sound must be a property of the cochlea. That is a conception which meets us at every turn and it is one which demands our closest attention. Let us conceive for a minute the auditory outfit implied by an acceptance of Helmholtz's theory. Let us imagine a chamber fitted with 15,000 resonators, each resonator connected by its nerve or telephone wire with a corresponding nerve-station in the brain. These 15,000 nerve-stations we must suppose to be connected with a common central exchange situated in the cortex of the brain—where sound rises into the field of consciousness. Let us suppose a complex series of sounds reaches the resonator chamber; each sympathetic resonator sends messages to its respective nerve-station; these stations, thousands in number, forward the messages to the central cortical exchange which has to deal with them. The central exchange has only one key or clue to the particular station or stations from which the messages come: namely, the rate at which stimuli or messages arrive; the final process of analysis must be done in the cortex of the brain even if von Helmholtz's theory be true.

Now on your theory there is a receiving chamber, but it is fitted with only one great receiver. There is only one great cable—the auditory nerve and tract—which conveys to the centre of hearing the messages received, exactly in the order and in the time relationship with which they are produced in the internal ear, and when they arrive in sequence at the centre for hearing in the cortex of the brain, they are sorted out according to the time intervals which separate them. Such a task places no more on the centre of hearing than von Helmholtz had done when he expected it to recognise each of the 15,000 nerve-stations by the number of stimuli or vibrations they sent in per second. Indeed you make a smaller demand on the hearing centre—one which is in conformity with the demands which are made on the centres for sight, smell, and taste. In formulating his theory of hearing, von Helmholtz thought to bring that sense into line with the theory which Thomas Young had formulated for vision. Young had postulated three kinds of nerves for the retina ; von Helmholtz went a considerable degree further and postulated many thousands of different kinds of nerves for the ear. The most impossible aspect of von Helmholtz's theory comes to light when we carry it beyond the cochlea—into the nervous system. The final process of analysis must lie in the brain : all you expect of the cochlea is that it will supply the brain with the requisite data from which an interpretation of sound can be made. In my opinion you have succeeded and have thus established a really satisfactory theory of hearing. I am, etc.,

A. Keith.

AN APPENDIX ON THE STRUCTURES CONCERNED IN THE MECHANISM OF HEARING.

By ARTHUR KEITH, M.D., F.R.S.

Part I

The Growth of our Knowledge concerning the Internal Ear.

In order to make clear how we have come by our present knowledge of the structure and mechanism of the ear, I propose to go back a hundred years and see what medical students of that time were taught concerning the organ of hearing. At that time the standard text-book in England was the "Anatomy and Physiology of the Human Body," by John and Charles Bell, of which the first edition was issued at Edinburgh in 1793. It is, however, from the sixth edition I am to quote, issued in 1826: for that edition Sir Charles Bell was entirely responsible. Time has shown that he had obtained a deeper and truer insight of the human body than any other Briton of his time, and it is therefore of importance to see what he taught concerning the ear. I reproduce in Fig. 1 an illustration which shows clearly and concisely his conception of how the various parts of the ear served to convey sound-vibrations to the nerve terminals. He pictures the drum set at the end of the ear passage as a vibrating membrane;

he shows how the chain of ossicles in the middle ear, or tympanum, conveys the vibrations of the drum to the inner ear; he depicts the inner ear or labyrinth as a complicated but closed cavity filled with fluid. He recognised, too, the importance of the round window of the inner ear (Fig. 1). He saw that it would be impossible for the foot-plate of the stapes, which is set in the oval window of the inner cavity or labyrinth of the ear (Fig. 1), to move unless there was also a round window. It is best to let Sir Charles Bell speak for himself:—

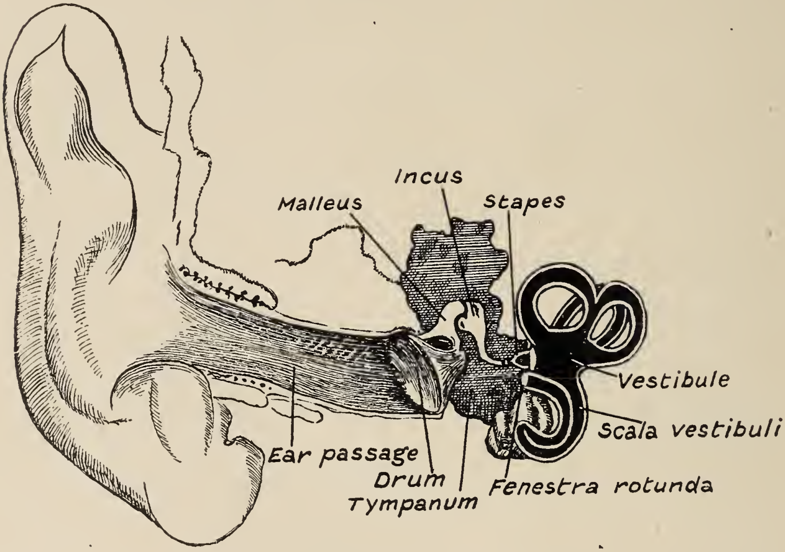

Fig. 1.—Illustration by Sir Charles Bell showing his conception of the structure and mechanism of the human ear. In the figure, as reproduced here, two of his illustrations are combined.

"But if the fluid of the labyrinth be surrounded on all sides; if, as is really the case, there can be no free space in the labyrinth, it can partake of no motion, and is ill suited to receive the oscillations of sound. Against this perfect inertia of the fluids of the labyrinth I conceive the *foramen rotundum* is set as a provision. It has a membrane spread over it, similar to that which covers the *foramen ovale*. As the *foramen ovale* receives the vibrations from the bones of the tympanum or middle ear, they circulate through the intricate windings of the labyrinth and are again transmitted to the air in the tympanum by the *foramen rotundum*. Without such an opening there could be no circulation of the vibrations in the labyrinth. But, as it is, the provision is beautiful. The membrane of the *foramen rotundum* alone gives way of all the surfaces within the labyrinth and this leads the course of the undulations of the fluid in the labyrinth in a certain unchangeable direction."

We see, then, that Sir Charles Bell believed that the vibrating foot-plate of the stapes gave rise to mass displacements of the fluid filling the labyrinth, and his illustration (Fig. 1) shows that the displacement passed from the main chamber of the inner ear—the vestibule—to the round window by the two passages or scalæ of the cochlea —the upward or vestibular passage joining the downward or tympanic passage at the communication or helicotrema situated at the apex of the cochlea. The nerves which terminate on the partition between the two cochlear passages—the spiral lamina—he conceived to be stimulated by the fluid of the labyrinth, and thus the sensation of hearing was produced.

Men of Sir Charles Bell's time were perfectly familiar with the fact that the ear could analyse and separate the various elements of a mixed sound. It is of particular interest to see how he sought to explain this property of the ear to his students.

"We think that we find in the spiral lamina the only part adapted to the curious and admirable powers of the human ear for the enjoyment of melody and harmony. It is in vain to say, that these capacities are in the mind and not in the outward organ. It is true, the capacity for enjoyment, or genius for music, is in the mind. All we contend for is that those curious varieties of sound which constitute the source of this enjoyment are communicated through the ear, and that the ear has *mechanical* provisions for every change of sensation. There is no part of the proper organ which appears susceptible of the variety of musical notes but the spiral lamina of the cochlea. Its breadth is in regular gradations of parts from the base towards the point or apex, and whether the fibres (of the bony spiral lamina) were to be taken as the cords of a harp, or the tubes like the ora of a wind instrument, every gradation of sound may be supposed to have its corresponding organ to vibrate, and by its vibration to move a distinct part of the auditory nerve."

This statement of Sir Charles Bell has a triple interest: he seeks for an explanation of why the spiral lamina gradually increases in width as it ascends to the apex of the cochlea; he sees in it a resemblance to the increasing length of the strings of a harp; he foreshadows the "resonator" action of the cochlea.

In the year 1837, when Sir Charles Bell was approaching the end of his career, William Bowman, a young medical man trained in Birmingham and aged twenty-one, was appointed demonstrator of anatomy at King's College, London. The compound microscope was then becoming an effective instrument, and the younger and more enterprising medical men were beginning to use it to unravel the structure of the tissues of the human body. Sir William Bowman was one of these pioneers. His researches on the structure of the eye have become classical; but it is on account of his researches into the microscopic structure of the ear that he enters this narrative. I do not know when he began and completed this part of his inquiries, but it was in 1856 that he published an account of them.[1] I reproduce in Fig. 2, a combination of two of his illustrations in order to make clear the nature of his discoveries. They concern the minute structure of the spiral lamina which forms a partition between the two passages of the cochlea, and in which the fibres of the auditory nerve terminated.

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[1] See "The Physiological Anatomy and Physiology of Man," by R. B. Todd and William Bowman, vol. i, 1843; vol. ii, 1856. See vol. ii, p. 77.

It will be seen from his illustration that he recognises, as his predecessors had done, that the spiral lamina, as seen in a section across the cochlear passages, is made up

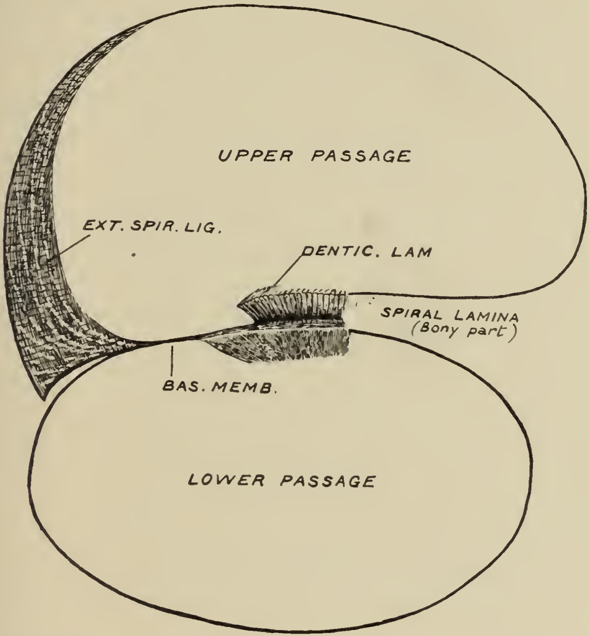

Fig. 2.—Sir William Bowman's drawing of the structure of the spiral lamina—the partition between the two passages of the cochlea.

of an inner or bony part, which is attached to the central column of the cochlea, and an outer or membranous part (Bas. memb. Fig. 2). His first discovery relates to a structure which he found situated on the upper or the vestibular surface of the bony lamina of the partition. " Being uncertain respecting the office of this structure," he writes, " we shall term it the denticulate lamina from a beautiful series of teeth forming its outer margin." (See Fig. 2.) He notes another fact about the denticulate lamina—one which has been rather overlooked in recent years, but which is true—namely, that in the basal coil of the cochlea the outer margin of the denticulate plate reaches only to the outer edge of the bony part of the partition, but as the plate is traced towards the apex of the cochlea it is found to project more and more beyond the margin of the bony plate (see Fig. 23, p. 235). His second discovery relates to the structure of the membranous part of the spiral lamina—the part now universally recognised under the name of the basilar membrane (Fig. 2). "This," he writes, "is a transparent, glassy lamina, having some resemblance to the elastic lamina of the cornea, and the capsule of the lens." I reproduce the drawing he made of the basilar membrane seen on its lower or tympanic surface as when examined by a microscope. He saw that the basilar membrane was made up of three zones or belts. "A narrow belt of it (see Fig. 3) next the osseous zone is smooth and exhibits no internal structure"; the middle and by far the wider belt "is marked by very minute straight lines radiating outwards." At its attachment to the outer wall of the cochlear passage there is a narrow, outer, clear belt or zone. He noted that the inner clear belt of the basilar membrane was "little affected by acids; it seemed hard and brittle"; the middle or pectinate (comb-like) zone was "more flexible and tore in the direction of its lines," while the outer zone was "swollen and partially destroyed by the action of acetic acid." He noted, too, the spiral vessel which passes along the under or tympanic surface of the basilar membrane (Fig. 3), "which resembled capillaries in the texture of its walls, but exceeds them in size. It is the only vessel supplied to the membranous zone and seems to me thus regularly placed that it may not mar the perfection of the part as a recipient and propagator of sonorous vibrations." The concluding part of this quotation is the only indication given us that Bowman regarded the basilar membrane as a vibrating structure.

Sir William Bowman made a third discovery which is depicted in Fig. 2. He noted that the basilar membrane was attached to a peculiar structure on the outer wall of the cochlear canal—one which clearly plays an essential part in the mechanism of hearing. Nowadays we call this outer structure, which binds the basilar membrane to the outer bony wall of the cochlear canal, the external spiral ligament. Bowman gives the following description of it: "At its outer or convex margin the membranous zone is connected to the outer wall by a semi-transparent structure. This gelatinous-looking tissue was observed by Breschet and is indeed very obvious on

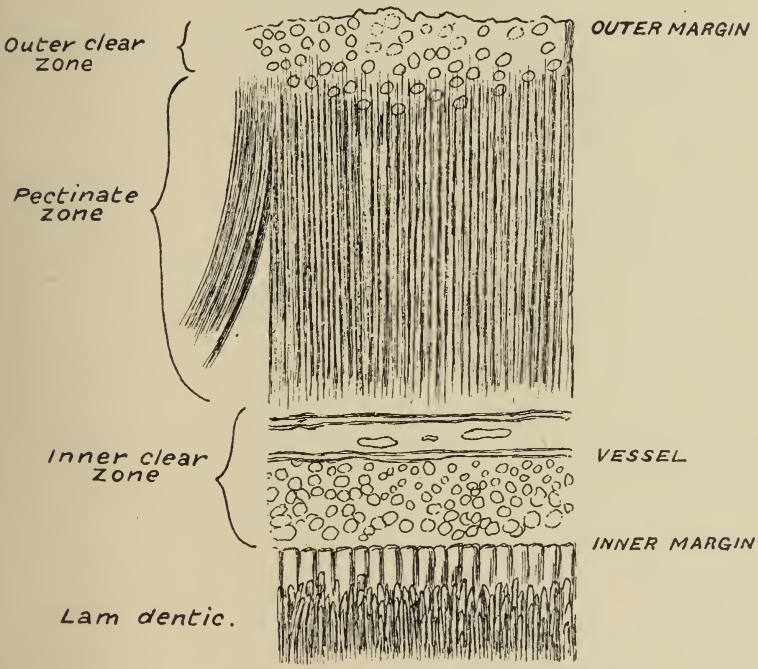

Fig. 3.—From Sir William Bowman's drawing of the basilar membrane—as viewed on its lower or tympanic surface through a microscope.

opening the cochlea; but we are not aware of any one having hinted at what we regard to be its real nature." In Bowman's opinion, the outer spiral—or, as he named it, the cochlear—ligament was largely composed of unstriped or involuntary muscle fibres which were designed for altering the tension of the basilar membrane, thus protecting the delicate cochlear nerves from injury. The muscle fibres ended, he believed, in the outer clear zone of the membrane. Later and more accurate methods have shown that Sir William Bowman was mistaken as regards the muscular nature of the external spiral ligament; it is composed of fibrous tissue which has no power of active contraction; and he was also wrong about the termination of the nerves. Bowman noted the important fact that this ligament diminishes in size and strength as one passes from the base to the apex of the cochlea. The only one, so far as I know, who has called attention to the functional importance and structural features of the external spiral ligament since Bowman's time is Dr. Albert Gray, of Glasgow; to his observation I shall return at another point in my narrative. It is clear that in any theory of hearing which is to gain our whole-hearted support we must be able to account for the denticulate lamina, the triple zones of the basilar membrane and the external spiral ligament, all of which were seen and described by Bowman.

While Bowman was carrying out his researches at King's College much more important discoveries were being made by a young Sardinian nobleman—the Marchese Alfonso Corti.[1] After taking a degree in Medicine at Padua, he went to Vienna in 1845 to study under Hyrtl, the anatomist, and then to research in Germany under Koelliker, and it was while working with that great master of microscopical technique that Corti stumbled on the essential part of the cochlea now known as the organ of Corti.

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[1] For an account of Corti and his work, see *Anatomischer Anzeiger*, 1914, vol. xlvi. p. 368.

While making a study of nerve cells he was led to examine those which are placed on the auditory nerve within the cochlea, and discovered a new collection of them set on the fibres which enter the spiral lamina of the cochlea. It was while thus engaged that he noted a peculiar and complex structure set on the upper or vestibular surface of the membranous or basilar part of the spiral lamina. How such a structure escaped Bowman's notice one cannot now tell. Corti was still under thirty years of age when, in 1851, he published a full and accurate account of his discovery; his account thus preceded that of Sir William Bowman by five years. Soon after the announcement of his discovery, Corti became affected with phthisis, gave up anatomy, returned to Italy, and there settled on his vineyards, dying in 1876, at the age of fifty-four.

I can best make clear the nature and importance of Corti's discovery by reproducing, not one of his illustrations, but one by the greatest living authority on the structure of the ear—Professor Gustav Retzius,[1] of Stockholm. The illustration (Fig. 4) shows a section across the middle turn of the cochlea with Corti's organ situated on the upper or vestibular surface of the basilar membrane. In it Corti recognised three essential elements: (1) certain cells set in the organ, with fine hair-like processes projecting on its upper surface—the hair cells; (2) he observed that the organ was strengthened by rather stiff short fibres set one against another in the form of an arch—these fibres have unfortunately been given the name of "rods," which conveys a misleading idea of their nature; (3) he found that an exceedingly delicate membrane was attached to the upper surface of the denticulate lamina and lay over, and was attached to, the surface of the organ on which the hair-like processes projected. That structure, at first known as Corti's membrane, is now universally named the tectorial or covering membrane (Fig. 4). If Bowman had known of Corti's researches he would have had a clue to the meaning of his "denticulate lamina"; the tectorial membrane is attached to the lamina much as a nail is fixed to its bed on the tip of a finger; only the membrane differs altogether from a nail in being of a gossamer-like texture, and almost as sensitive and mobile as a fluid, and yet endowed with a high degree of elasticity.

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[1] In 1881 Prof. Retzius issued, at his own expense, a magnificent work, "Das Gehoerorgan der Wirbelthiere," containing an account of his extensive researches on the structure of the ear in vertebrate animals.

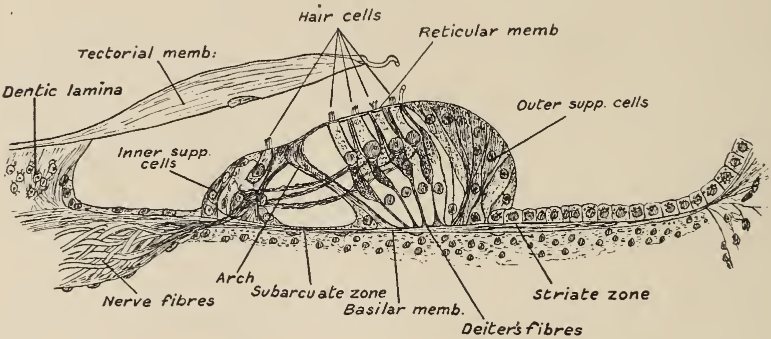

Fig. 4.—The organ of Corti as represented by Retzius—from the middle turn of the human cochlea. The tectorial membrane is represented as torn off the surface of the organ.

When we turn to Retzius' illustration (Fig. 4) we see that the nerve fibres are traced to definite terminations in the organ of Corti. After passing to the free edge of the spiral plate of bone, by canals which radiate outwards in that plate, the nerve fibres reach and perforate the basilar membrane opposite the inner attachment of the fibre arch of Corti, and then pass, in a curious spiral manner, to end in fine branches round the hair cells. Corti believed that the nerves ended on the under or tympanic surface of the basilar membrane; their true termination was not discovered until a somewhat later date, when improved methods of staining nerve tissues had been introduced. Nor was he aware of the true nature of the hair cells; he did not know that they were sensory in function, and that only through them could vibrations caused by waves of sound be converted into nerve stimuli.

In a few years Corti's contemporaries filled in the details of his discovery. Koelliker showed that the upper or tectorial surface of the acoustic organ or papilla was stiffened by a covering of exceedingly minute and delicate plates, forming a net-like or *reticular membrane* (Fig. 4). Deiters showed that, besides the arch-like arrangement of stiffening fibres described by Corti, there were others, formed in cells which were situated deep to and between the hair cells. These supporting fibres—Corti's fibres, Deiters' fibres—are attached at their deeper ends to the basilar membrane, and by their upper or more superficial ends to the reticular membrane (Fig. 4). These structures form an exceedingly delicate, flexible scaffolding or framework in which the essential parts—the hair cells and terminal nerve fibres—receive a setting and a support. The organ of Corti was thus found to be provided with a certain degree of rigidity and elasticity.

One other important advance in our knowledge of the cochlea needs mention. In 1854, three years after Corti's original paper had appeared, Dr. Reissner, who had been investigating the condition of the inner ear during stages of its development, observed that a membrane or delicate septum crossed the upper or vestibular passage of the cochlea, shutting off that part of the vestibular passage in which Corti's organ is situated (Fig. 9, p. 192); he believed it was only present in the embryo; Koelliker, however, demonstrated that it was also constantly present in the adult cochlea. The organ of Corti is therefore enclosed in an intermediate passage of the cochlea—the scala media (see Fig. 9). Further, the liquid which fills that passage and bathes the organ of Corti is of a different nature from that which fills the other two passages; it is secreted by a special vascular body situated on the outer wall of the scala media (see Fig. 9).

How von Helmholtz advanced our Knowledge.

Our knowledge of the cochlea had almost reached the stage just described when an important event occurred. In the year which saw the publication of Bowman's researches on the ear—1856—Herman von Helmholtz, at the age of thirty-five, was transferred from the University of Königsberg to that of Bonn. At Königsberg his researches chiefly concerned optics and the eye; when he reached Bonn, he settled down to extend our knowledge of acoustics and of hearing. It is important to note that he approached the problems of the ear as a physicist rather than as an anatomist. He summed up his researches on sound and on the ear, and issued them in 1863 as a book—one which at once became, and has justly remained, the standard work for everyone who applies himself to the study of hearing. I reproduce here a passage which is important for our present purpose because it reveals the point of view from which he approached the study of the ear:—

"This analysis of compound into simple pendular vibrations is an astounding property of the ear. . . . When we turn to external nature for an analysis of periodical motions into simple motions *we find none but the phenomena of sympathetic vibration.*"[1]

We see, then, that when Helmholtz set out to make his researches on the ear he was convinced that there was only one means by which the ear could carry out its analytical functions, namely, by a system of resonators. As is well known, he at first regarded the system of arches formed by Corti's fibres as such a system ; their dimensions change as Corti's organ is traced from the base towards the apex of the cochlea (Fig. 23, p. 235); they are set close to the hair cells ; the cells must be stimulated by the vibration of the arches. In the third edition he abandoned this view of the functional nature of the arches. Hasse had shown by then that the cochlea of birds was destitute of such arches and yet had the power of analysing sounds. He therefore adopted Hensen's opinion, that a resonator system was to be sought in the fibres of the basilar membrane itself. In the cochlea of a newly-born child—the cochlea has reached its full size at birth—Hensen found that the width of the basilar membrane, where it commenced at the base of the cochlea, was only 0·041 mm. ; its width increased rapidly in the basal part of the membrane, then slowly, until ultimately, at the apex of the cochlea, it became 0·49 mm.—twelve times as wide as it is at the commencement. These measurements of Hensen are still quoted in our leading text-books ; they were the measurements which Helmholtz accepted from Hensen, but they differ considerably from what have been observed by other anatomists. Retzius gives the width of the membrane near its commencement at the base of the cochlea as 0·21 mm. and near its termination at the apex 0·36 mm. ; at Sir Thomas Wrightson's instigation I have made measurements of four specimens of the human cochlea and found the basilar membrane to be 0·17 mm. at the commencement and 0·400 mm. at its termination. At the very most the width of the basilar membrane is less than three times as wide at its termination in the apex as at its beginning in the base of the cochlea.

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[1] Page 189 of Ellis's translation (1875) of "Die Lehre von den Tonempfindungen," 3rd edition, 1870.

I have already cited the description of the basilar membrane which Bowman published in 1856 (Fig. 3). When the thin, transparent, glassy membrane was treated with certain reagents he noticed that the middle wider zone was scored with lines, and was comb-like or pectinate in appearance, while the inner and outer zones remained apparently structureless. Corti's discovery made the relationship of Bowman's three zones perfectly clear (see Fig. 4). The inner zone lies under the arch formed by Corti's arch fibres and hence is now known as the subarcuate or arcuate zone, while Bowman's pectinate or striate zone stretches from the foot-plate of the outer fibres of the arch to the external spiral ligament. Bowman's outer zone proves to be, in reality, an intrinsic part of the external spiral ligament. Hensen found that the parallel lines of Bowman's pectinate zone were due to the fact that it was made up of very minute, delicate fibres (0·003 mm. in diameter) which run parallel to each other from the outer foot-plates of the arch to the external spiral ligament. The fibres are packed tightly together, laid closely side by side, within the substance of the basilar membrane, and are about 16,000 in number. Retzius found them rather more numerous (24,000). It was the fibres of the pectinate zone—stretching from the outer foot-plates of the arch to the external spiral ligament—which Hensen recommended to Helmholtz as a possible system of resonating strings. I observed that the width of the pectinate zone and therefore the length of the resonating fibres near the commencement of the basilar membrane was 0·120 mm. and almost at its termination in the apex of the cochlea 0·300 mm. The corresponding measurements given by Retzius are 0·140 mm. for the commencement, 0·240 for the termination; Henle found a much greater difference between the basal and apical fibres, namely, 0·023 at the base and 0·410 at the apex. The specimen examined by Henle must have been exceptional. Ultimately, then, Helmholtz selected the pectinate part of the basilar membrane as a resonator system.

Helmholtz's language is so clear and definite and Ellis's translation is so good that I cannot refrain from quoting the passage with which Helmholtz opens his discussion on the anatomy of the ear :—

"Now suppose we were able to connect every string of a piano with a nerve fibre in such a manner that this fibre would be excited and experience a sensation every time the string vibrated. Then every musical tone which impinged on the instrument would excite in the ear, as we know to be really the case, a series of sensations corresponding to the pendular vibrations into which the original motion of the air had to be resolved. By this means, then, the existence of each partial tone would be exactly so perceived, as it is really perceived by the ear. The sensations excited by the higher partials would, under the supposed conditions, fall to the lot of different nerve fibres, and hence be produced perfectly, separately and independently. Now as a matter of fact later microscopic discoveries respecting the internal construction of the ear lead to the hypothesis that arrangements exist in the ear similar to those which we have imagined. The end of every fibre of the auditory nerve is connected with small elastic parts which we cannot but assume to be set in sympathetic vibration of the waves of sound."

Von Helmholtz's Conception of the Mechanism of the Organ of Corti.

With this hypothesis in his mind, Helmholtz set to work to see what *rôle* the various elements in the organ of Corti would play in converting sound vibrations into nerve stimuli. I have attempted in Fig. 5 to give an accurate representation of the manner in which he believed the various parts did work. I have represented a single arch of Corti, but it must be remembered that the outer and inner pillars do not meet exactly to form single arches ; the opposite fibres meet irregularly, there being about 6,000 inner arch fibres or pillars (5,590 is

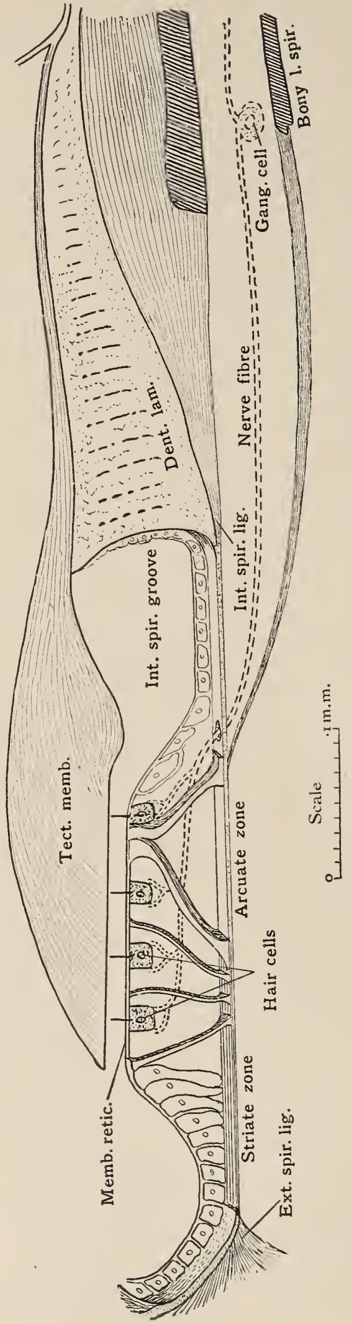

Fig. 5.—A diagrammatic section across the organ of Corti to show Helmholtz's conception of its mechanism.

Retzius' exact estimate) to about 4,000 outer arch fibres (3,848 according to Retzius). I take a single separated arch because the more complex system of reality fits less easily into the conception of the mechanism of the organ of Corti formulated by Helmholtz. As there are about 20,000 fibres in the pectinate zone of the basilar membrane (16,000 Hensen, 24,000 Retzius), there are, therefore, five fibres for each arch; the outer foot-plate of an arch will be attached to the external spiral ligament by a segment of the basilar membrane which contains about five fibres (see Fig. 5). The arch is situated over the clear inner zone (subarcuate zone) of the basilar membrane, which shows no evidence of being composed of linear fibres.

The Fixation of the Basilar Membrane.

It is of importance to note the exact manner in which the basilar membrane is attached internally to the edge of the spiral bony plate (see Figs. 5 and 6). It has to be fixed in such a way as will protect the fine leashes of nerves which issue from the edge of the bony plate and then pass inwards to end in the organ of Corti. It will be seen from Fig. 5 that, internal to the inner foot-plate of the arch, the homogeneous structure of the basilar membrane is retained, but it is increased in thickness and in strength as it lies beneath the floor of the inner spiral groove. As the inner attaching layer passes under the denticulate lamina, which is internal to the groove (Fig. 5), the stratum, which represents the internal continuation of the basilar membrane, becomes opened out into a distinct brushwork of fibres—the stronger ones passing directly to the bony lamina, where they are attached above the opening by which the nerves escape from the bony lamina (Fig. 5). Other fibres of the basilar brushwork will be seen to end on the dense fibrous mass which lies below the denticulate lamina ; this fibrous mass is bound to the upper surface of the bony lamina. On the other hand, it will be noted that an open sponge-work of fine fibres and clear spaces lies between the denticulate lamina and the fibrous bond just described on the upper surface of the bony plate (see Fig. 5). That sub-denticulate sponge-work is constantly present and must be an essential part of the cochlear mechanism. It is of some importance to note also that a small spray of fibres turns upwards to the denticulate lamina at the inner side of the internal spiral groove (Fig. 5).

Under shelter of the structures just described, a leash of nerves is seen (Fig. 4) to issue from the canal in the bony lamina, its fibres passing inwards until they almost reach the inner foot-plate of the arch where they perforate the basilar membrane (Fig. 5). At the point of perforation it will be seen that an additional strand springs from the sheath on the under or lower side of the nerve leash and joins the basilar membrane ; this lower strand gives the membrane an attachment to the lower edge of the spiral bony plate (Fig. 5).

I have gone minutely into the exact attachment of the basilar membrane to the bony lamina because neither Helmholtz nor any of his successors has made an exact study of it. In any system of vibrating strings the manner of attachment is clearly important. To the various parts of the internal attachment of the basilar membrane—all that lie internal to the inner foot-plate of the arch—I propose to give the name of *internal spiral ligament.*

The external spiral ligament—the structure by which the basilar membrane is fixed to the outer wall of the cochlear passage—is equally important if we are to understand the mechanism of a vibrating membrane. It has not received the study it deserves. Just above the outer attachment of the basilar membrane there is a shallow groove—the external spiral groove—which passes right from the beginning to the end of the cochlea (see Fig. 23, p. 235). When looked at from above, the groove is seen to be puckered—depressions and ridges alternating in its floor and sides ; Bowman noted those puckers and ridges. Along the upper margin of the groove there is a prominence or crest known as the external spiral crest (Fig. 6). The crest is composed of fibres and cells tightly packed together : many of the fibres, in such a section as is shown in Fig. 6, are cut across, for they run along the crest. Now the crest has an extremely important relationship to the basilar membrane. In Fig. 6 it will be seen that the membrane is really continued up beneath the floor of the spiral groove to end beneath the internal spiral groove, forming the main part of the internal spiral ligament. When the basilar membrane is stripped away from the cochlea, it carries at its outer margin the continuation which lies in the floor of the external spiral groove—the part named by Bowman the outer clear zone. The moment the basilar membrane reaches the lower border of the spiral groove its structure changes ; the fibres cease and their place is taken by a homogeneous membrane—Bowman's outer clear zone.

While the main external attachment of the basilar membrane is to the spiral crest, there are other attachments which are manifestly of importance. If Fig. 6 is examined it will be seen that very fine, tensely stretched fibres spring from the homogeneous stratum just described in the floor of the external spiral groove and radiate out into the substance of the external spiral body,

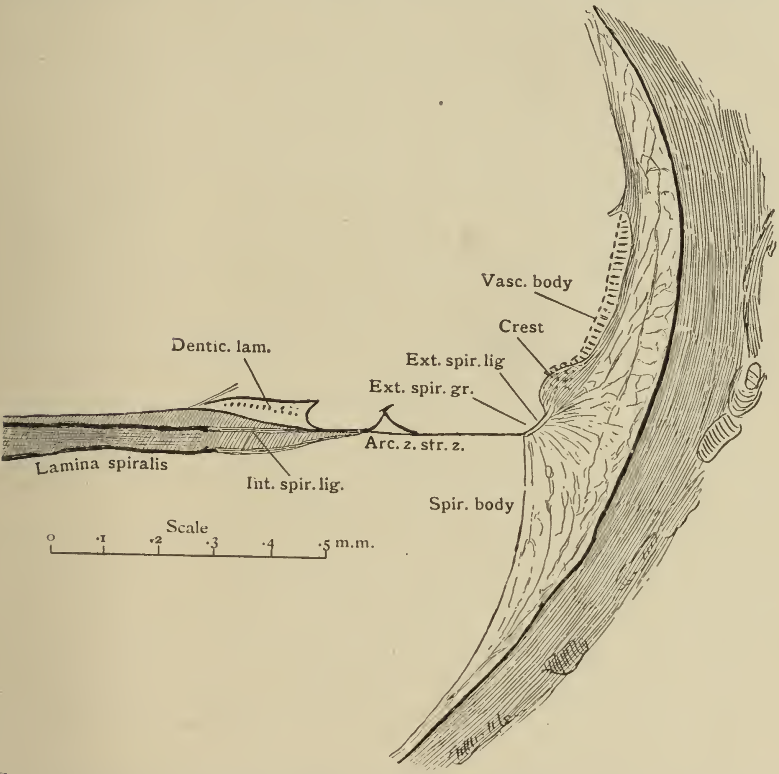

FIG. 6.—Section across the middle turn of the human cochlea to show the external spiral body and attachments of the basilar membrane. Arc z= arcuate zone ; str. z=striate zone.

the early ones downwards, the later ones upwards and outwards, and the intermediate in a transverse direction. The lowest of these radiating fibres—those lying immediately beneath the lining membrane of the tympanic passage—spring directly from the outer end of the striate zone. I noticed, too, that the descending series of fibres is strong and numerous at the commencement of the spiral body at the base of the cochlea, but this series gradually becomes less in number and in strength as the apex of the cochlea is reached. It is important to note, also, that the external as well as the internal spiral groove becomes wider and shallower as the cochlea is ascended (see Fig. 23) ; the homogeneous continuation of the basilar membrane lying in the floor of these grooves becomes longer and thinner. I would confine the name *external spiral ligament* to the homogeneous layer and the radiating system of fibres. The ligament ends in the external spiral body—an open-meshed, fibrous structure by which the ligament is fixed firmly to the outer bony wall of the cochlea. Thus the basilar membrane is swung right across the cochlear passage, secured at either end by fastenings of an elaborate nature.

I have described the strong and elaborate fastenings of the basilar membrane. There is one feature of these fastenings—of both the outer and inner ones—on which I have scarcely laid enough emphasis. I must believe that the homogeneous strata—representing the outward and inward continuations of the basilar membrane into the spiral ligaments—have elastic properties to a high degree. Bowman's inner (subarcuate) zone, which is continuous with the inner spiral ligament, is of the same nature. These homogeneous layers do not give the staining reaction which yellow elastic tissue does, but their structure indicates their real nature. The basilar membrane, then, is fixed at its margins by tissues having the character of elastic tissue.

Is the Tension of the Basilar Membrane regulated by the Stria Vascularis?

I have mentioned the attachment of the homogeneous continuation of the basilar membrane to the spiral crest (Fig. 6). It will be observed, however, that the spiral crest is but the lower end of a peculiar vascular structure implanted in the upper part of the spiral body. This vascular structure—designated by a name which is misleading, the *stria vascularis*—is enclosed, as seen in section (Fig. 6), between two fibrous coats, an inner one, delicate and perforated, and an outer, very strong and thick, the latter suddenly increasing in bulk and substance at the lower end of the body to form the spiral crest. The space between the coats is filled by loosely packed epithelial cells which have always been regarded, and I have no doubt rightly, as the gland for secreting the fluid (endolymph) which fills the scala media and bathes the organ of Corti. Arteries of minute size enter the spiral body from above; their finer branches perforate the outer capsule of the vascular body and ramify among the epithelial cells. From the vascular body emerges a rich plexus of minute veins with very thin walls; they perforate the outer capsule and descend in the spiral body to make their exit from the cochlea in the floor of the tympanic passage. I cannot believe the connection of the basilar membrane to the vascular body to be of no significance; to me a functional relationship is implied. At first I imagined that the capillaries within the body might become engorged; the capsule would thus become distended and thereby shortened, so that a tension or tightening of the basilar membrane would result. To produce such an effect it would be necessary for the veins, which emerge from the body, to have a strong muscular coat, so that they might become constricted and thus dam the blood back. They are destitute of a circular muscular coat and therefore cannot have such an effect as I imagined, and yet I cannot do otherwise than maintain the opinion that, however regulated, the tension in the vascular body must affect the tension of the basilar membrane. In no other way can we explain its strong outer coat and its direct connection with the basilar membrane. The vascular body, which is in reality a spiral, ribbon-like structure implanted on the outer wall of the scala media, scarcely alters in size until the apical region of the cochlea is reached.

The Arch Pillars or Rods of Corti.

Having thus established the exact fixation of the strings which were regarded by Helmholtz as a vibrating system, I now proceed to build up a picture of the organ of Corti and show the manner in which Helmholtz believed the vibrations were transmitted to the hair cells and thus to the auditory nerves. A single arch (see Fig. 5) is set up, with the outer foot-plate fixed to five fibres. The inner foot-plate is planted at the commencement of the internal spiral ligament; the arch spans the inner structureless zone (subarcuate). At the apex of the arch the fibre pillars become thickened, strengthened and bent; their upper ends fit into each other, as is shown in Fig. 5. I have never seen an open cleft or clear line of separation between the heads of the fibres; they are firmly attached, but I suspect, without being able to demonstrate it, that some degree of movement independent of the bending of the pillars is possible at the apex of the arch. From the head of the inner fibre a fine horizontal flange projects inwards, to which an inner hair cell is attached (Fig. 5); from the outer, a similar horizontal flange or plate passes outwards, to which the innermost of the outer hair cells is attached. The arch thus carries and supports two of the four hair cells (the number usually seen on a single section), and they are probably the two which are the most important from a functional point of view.

The other Parts in the Framework of the Organ of Corti.

The arch is only part of the delicate skeleton of Corti's organ. It will be noticed there are really three distinct parts in each fibre or pillar of the arch : (1) the foot-plate fixing the pillar to the basilar membrane ; (2) the supporting or oblique part, forming one side of the arch ; (3) the surface flange at the upper end for the fixation and protection of a hair cell. External to the arch, there are to be seen, in an ideal section, three other fibres formed by supporting cells—Deiters' cells. They are planted on the striate part of the basilar membrane (Fig. 5) ; their fibres are more delicate than those of the arch. As Deiters' fibres rise to the surface of Corti's organ they expand, like the pillars, into fine plates or phalanges. The phalanges of the arch and of Deiters' fibres form an extremely delicate jointed armour—the membrana reticulata—on the upper surface of Corti's organ. Between the outer three phalanges I have set the remaining two outer hair cells, which can be recognised when an ideal section across Corti's organ is examined. We have thus a flexible, skeletal system supporting a series of cells which act as stations for receiving auditory stimuli.

Supporting Cells.

To complete Corti's organ, it is necessary to load the vibrating fibres still further. External to the supporting fibres of Deiters' come a series of cells (Fig. 5) which serves as an outer support. Each of these cells has a delicate supporting membrane or envelope. The armour plating of phalanges—the reticular membrane

—fades away in the covering of the outer supporting cells. Likewise, internal to the arch there is an inner supporting series of cells, smaller in size and fewer in number than the outer series (Fig. 5).

The Tectorial Membrane.

The machinery of Corti's organ is complete when we place the tectorial membrane in the position which Helmholtz believed it to hold to the organ of Corti (Fig. 5). With that addition we have before us the completed mechanism required for the transmutation of sound vibrations into nerve stimuli. If the basilar fibres depicted in Fig. 5 are set in vibration, then it is clear that the arch and supporting fibres resting on them will also be set in motion; so will the hair cells, carried in the reticular membrane; as the basilar fibres vibrate upwards and downwards, the hair cells will move with them; at the end of every upward excursion the cilia will hit against the tectorial membranes, and thus an auditory stimulus will be produced. The tectorial membrane was treated by von Helmholtz as if it were a stationary structure.

To make Helmholtz's conception of the mechanism of Corti's organ clear from a physiologist's point of view, it is convenient to identify, on a tracing representing the vibrational waves of a simple tone, the various movements of the stapes and of the basilar membrane. Sir Thomas Wrightson has given a completely novel interpretation, and I am convinced the right interpretation, but I am here dealing with von Helmholtz's interpretation—the interpretation which is universally accepted at the present time. Thus in Fig. 7. *A.* four phases are marked: phase I, the rise from (*a*) on the zero-line (*x*—*x*) to the crest (*b*); phase II, the fall from the crest (*b*) to the zero line at (*c*); phase III, the fall from the zero line at (*c*) to the trough at (*d*) ; phase IV, the rise from the trough of the wave at (*d*) to the zero line at (*a*). Still following Helmholtz we may identify the same four phases in a complete stapedial cycle—phase I, the inward movement from zero or rest position in the fenestra ovalis to the inward limit ; phase II, the retreat outwards to zero position ; phase III, the continued outward movement from zero to the outward limit ; phase IV, the return to zero position in the fenestra. Likewise in a complete vibrational excursion of the basilar membrane four corresponding phases may be recognised (Fig. 7. *B.*) phase I, the descent of the basilar membrane from zero level (*a′*, *c′*, *a′*) to the lower limit (*b′*), caused by the inward movement of the foot-plate and displacement of cochlear fluid in the vestibular passage ; phase II, the rise of the membrane to zero level, resulting from the outward movement of the stapedial foot-plate (c^1) ; phase III, the ascent of the membrane to the upper limit (d^1), due to the continued outward movement of the foot-plate ; phase IV, the return of the membrane to the resting phase, corresponding to the first part of the inward stroke of the stapes. According to this—an erroneous but usually accepted interpretation—phases II and III in the sound wave correspond to the whole of the outward movement of the foot-plate of the stapes and the ascent of the basilar membrane from b^1 to d^1 (Fig. 7. *B.*) ; phases IV and I in the tracings to the inward movement of the foot-plate and downward movement of the basilar

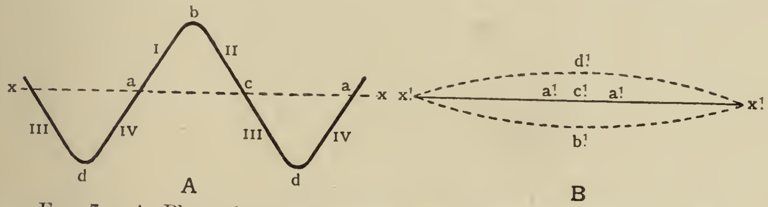

Fig. 7.—*A*. Phases in a conventional tracing representing a sound wave.
Fig. 7.—*B*. Corresponding phases in the movements of basilar membrane according to the interpretation given by von Helmholtz.

membrane (from d^1 to b^1). In Helmholtz's scheme only one stimulus is produced in each cycle of basilar movement, and that is at the close of phase III (at d^1), when at the end of the ascent of the basilar membrane the cilia were thrust against the tectorial membrane (see Fig. 5). Helmholtz, however, did not concern himself with the movements of the basilar membrane as a whole. For him it was divided into a series of elements or segments, some 4,000 in number, each being constituted after the scheme shown in Fig. 5. Each segment of the membrane had a power of independent vibration; it responded only to sound waves of a definite length; each segment had its own hair cells and its own nerve fibres; we must suppose, further, that each segment had its own end station in the ganglionic cell masses of the brain, and that the stimulation of a very small number of hair cells and nerve fibres was sufficient to rouse sensation in the auditory centres of the brain. When a simple tone was sounded, only the segment or segments of the basilar membrane in sympathy with that tone responded, and only the nerve fibres of that segment and the corresponding end station in the brain were stimulated and excited.

There are no Anatomical Structures which can serve as Resonators in the Cochlea.

Helmholtz was fully aware of the anatomical difficulties with which his theory was beset. That is shown by the following passage.[1]

"On reviewing the whole arrangement there can be no doubt that Corti's organ is an apparatus for receiving the vibrations of the basilar membrane and for vibrating of itself, but our present knowledge is not sufficient to determine with accuracy the manner in which these vibrations take place: For this purpose we need to estimate the stability of the several parts and the degree of tension and flexibility, with more precision than can be deduced from such observations as have hitherto been made on isolated parts, as they casually group themselves under the microscope."

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[1] Page 211, Ellis's translation.

In the forty-seven years which have elapsed since Helmholtz penned this sentence our knowledge of the minute structure of the cochlea has been greatly extended, and although we have not yet succeeded in estimating exactly "the stability of its several parts and their degree of tension and flexibility," we are in a position to make approximate estimates of these qualities. In the last edition of Koelliker's "Geweblehre" (1902), von Ebner sums up the conclusions that anatomists have come to as regards Helmholtz's theory: "However unwilling we are," he writes, "we must give it up." Helmholtz knew that the basilar fibres are not free in the manner diagrammatically represented in Fig. 5, but are packed tightly together side by side and embedded in a semi-fluid cementing substance; he knew they were clothed on their lower surface by a layer of loose cells and fibres and that their upper surface was covered by a stratum of cells. The basilar fibres are not free strings. He knew, too, that the pillars of neighbouring arches were bound tightly together at both their foot-ends and head-ends; he knew that if one pair of arches vibrated, the neighbouring arches must move with them; but he supposed they would move to a less degree. He did not know, however, that each segment had not its own independent supply of nerve fibres. Held found that a single fibre may be distributed along a quarter of a turn of the cochlea, including a series of some 300 or 400 arch segments. Such a distribution is incompatible with the resonator theory.

The brilliant manner in which Helmholtz expounds his theory, and the marvellous way in which the various phenomena of hearing are explained by his theory, carry the reader away in a flood of conviction. It is only when we begin to make a minute study of the structure of the cochlea and try to explain the use of its various parts on the basis of Helmholtz's hypothesis, especially when we try to conceive the various parts acting in the manner postulated by Helmholtz, that we begin to realise that, although he had done more than any man to place the sense of sound on a basis of science, he had not succeeded in discovering the manner in which sound waves are converted into nerve stimuli within the human ear. On his theory, an elaborate mechanism like the organ of Corti is unnecessary. In the third edition of his work on Auditory Sensation, Helmholtz cited the experiments which von Hensen had made on the free auditory hairs of a crustacean (the opossum shrimp). Von Hensen discovered that " certain tones set some hairs into vibration and other tones other hairs." The hairs acted—as Helmholtz supposed the fibres of the basilar membrane did—as a system of resonators. If a system of resonators can be established so simply, an anatomist may well wonder why so complex a structure as the organ of Corti should have been elaborated for this purpose. There are cells with auditory hairs in the organ of Corti ; why were they insufficient to serve air breathing vertebrate animals as a system of resonators ? Such a system would have met every condition necessary for Helmholtz's theory in a much simpler manner than does the organ of Corti. Professor McKendrick has shown that pieces of watch spring, cut to suitable lengths, and set in a box filled with water, can be made to serve as a system of resonators in the same manner as the auditory cilia of a crustacean. On the other hand, if we suppose a compound wave of sound is resolved into its elements by the organ of Corti, not on the principle of resonators but on a totally different one, then, if we discovered that method, we should also obtain a full and satisfactory explanation of the organ of Corti.

PART II

The Structure and Mechanism of the Organ of Corti.

The manner in which the basilar membrane is interposed between the fenestra ovalis and fenestra rotunda.—I am of opinion that anatomists have failed to make clear to those who have no first-hand knowledge of the ear their difficulties in accepting the Helmholtz theory as the true explanation of the mechanism of the ear. In the first place, it is absolutely necessary to understand how the basilar membrane is placed in relationship to the footplate of the stapes on the one hand and to the membrane of the round window on the other. For this purpose I reproduce a drawing made from a series of microscopic preparations of a human cochlea—one of the specimens which was cut into microscopic sections during the course of the investigations carried out by Sir Thomas Wrightson and myself. It shows a slice across the basilar membrane—almost at its commencement. Here the membrane is narrow—160 μ[1] ($\frac{1}{158}$ of an inch). At one margin it is seen to be attached to the external spiral body—here particularly extensive and strong; at its inner margin it is fixed to the bony spiral lamina—here wide and thin. Below the basilar membrane is the lower end—almost the terminal part of the lower cochlear passage—the scala tympani. At this point, the floor of that passage is seen to be formed of a yielding membrane—the membrane closing the round window shutting the lower cochlear passage off from the cavity of the tympanum. Above the basilar membrane—we may omit from all our mechanical calculations the delicate yielding Reissnerian membrane seen over the basilar membrane—is the central chamber of the labyrinth—the vestibule—filled with fluid perilymph. The part of the vestibule seen immediately above the basilar membrane is that from which the upper or vestibular passage commences; indeed, that part of the vestibule really represents the commencement of the upper passage (see Fig. 8). The drawing also shows somewhat diagrammatically a section of the drum set at the end of the ear passage, the chain of bones crossing the tympanum, and the foot-plate of the stapes fixed in the oval window on the outer wall of the vestibule. Every inward movement of the drum causes an inward movement of the foot-plate with displacement of a certain amount of the fluid from the vestibule. Let us suppose that the septum represented by the basilar membrane and spiral plate, as shown in Fig. 8, is removed from the floor of the vestibule. Then when the foot-plate moves inwards there is no doubt as

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[1] $1000\ \mu = 1$ mm. $= \frac{10}{254}$ inch.

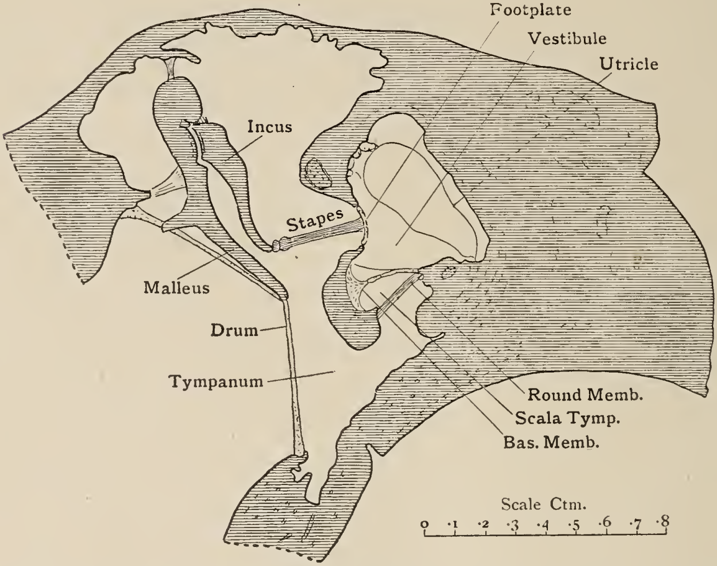

Fig. 8.—Section across the drum, ossicles, and cavity of the inner ear showing the vestibule in which the scala vestibuli commences and the terminal part of the scala tympani, the two scalæ being separated by the basilar membrane and Reissner's membrane.

to the direction which will be taken by the column of fluid which is displaced; it will descend, and the round membrane will be pushed downwards or outwards, thus bulging into the tympanum. The walls of the vestibule—of the whole labyrinth—are unyielding except at the round window. With the outward movement of the foot-plate the round membrane rises again into position. The fluid column—lying between the foot-plate and the round window—undergoes movements corresponding with those of the drum and of the sound waves which beat against the drum. Now suppose we replace the spiral plate and basilar membrane, as shown in Fig. 8. They form part of the column of fluid which lies between the foot-plate of the stapes and the round window. The basilar membrane is yielding and elastic. With the inward stroke of the stapes it will descend. The outward stroke of the stapes gives rise to a movement of the fluid and membrane in an opposite direction. Thus the basilar membrane, as shown in Fig. 8, becomes part of the column of fluid set in a vibratory movement between the foot-plate of the stapes and round window.

We obtain a still more direct knowledge of the mechanism of the organ of Corti from such a drawing as is shown in Fig. 9. A section across the cochlear passages is represented at a point about 18 mm. from the commencement of the basilar membrane in the floor of the vestibule and therefore near its middle point—for the basilar membrane, measured along its outer border, is from 35 to 40 mm. long. The basilar membrane, bearing the organ of Corti, and the bony plate of the spiral septum, are shown forming a partition between the upper and lower passages of the cochlea; for I am regarding the middle scala as if it were part of the upper or vestibular passage. At this point (shown in Fig. 9) the basilar membrane—measured from the point where the nerves pierce it at the inner foot-plate of the arch to its attachment to the external spiral body—

is 300 μ wide ($\frac{1}{84}$ in.). Now from measurements made on three specimens of the human cochlea I estimate that the average area of the membrana basilaris in man is 13·2 mm.^{2}; its average length 35 mm.; its mean width is approximately 0·333 mm., so that at the point chosen for representation in Fig. 9 the basilar membrane is under the mean width. It is also well to mention here the measurements which were made of the foot-plate of the stapes, in order that a clear opinion may be formed of how the stapedial area stands to the basilar area. The area of the foot-plate varies considerably—from 2·65 mm.^{2} to 3·75 mm.^{2}; I estimate that the average size in the adult is 3·2 mm.^{2}. The area of the membrana basilaris is thus nearly four and a half times that of the foot-plate. Now let us suppose the foot-plate to move inwards, displacing fluid from the vestibule into the upper or vestibular passage of

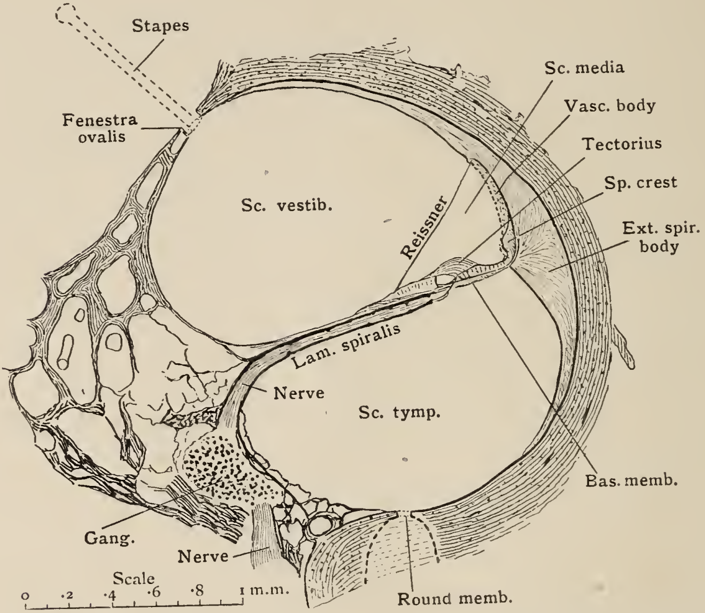

Fig. 9.—Section across the middle turn of the human cochlea, with certain adaptations explained in the text.

the cochlea; let such a movement represent a maximum inward excursion, which I suppose to be 0·050 mm. Sir Thomas Wrightson has shown in a former monograph (on the "Impulses of Compound Sound Waves," 1907) that the foot-plate does not move as a piston, but is loosely hinged at its lower border, a manner of fixation and movement also recognised by von Helmholtz. We may, therefore, regard $\frac{0\cdot050}{2}$ mm. as representing the effective maximum movement of the stapedial plate. If the displacement affects the whole extent of the basilar membrane, then the amount of downward movement of the basilar membrane—the extent of its depression into the scala tympani—will be equal to $\frac{1}{4\frac{1}{2}}$ of the stapedial excursion, namely, $\frac{0\cdot025}{4\cdot5} = 0\cdot0055$ mm.

In Fig. 9 I have tried to make the relationship of the stapes to the basilar membrane more evident. The oval window and foot-plate are supposed to have been drawn out into narrow strips or threads, so that they extend along the whole roof of the vestibular passages. The foot-plate of the stapes thus becomes a narrow thread of bone—only 0·091 mm. wide—let us say 90 μ. Further, in Fig. 9 I have stretched out the membrane of the round window, which has an average area of 2 mm.^{2}, into a narrow ribbon, 57 μ wide, and set it along the floor of the scala tympani. With such a diagrammatic arrangement we can best understand the manner in which the stapedial displacement acts on the organ of Corti. Let us now suppose the stapes as shown in Fig. 9 to execute a maximum movement inwards $\frac{50}{2}\mu$; as it moves in, the round membrane is pressed outwards to a corresponding extent by the displaced fluid—the outward movement of the round window in this case being $\frac{90}{57}$ of $25\mu = 35\mu$. Fig. 9 shows that the spiral lamina or septum is set between the stapedial plate and round membrane; it is made up of two parts—the greater part of a comparatively rigid bony plate, a small part by the thin elastic yielding membrane on which the organ of Corti is set. It is through the membranous part of the septum, here 300μ wide, that we suppose almost the whole of the displacement to take place. If the basilar membrane had a piston-like movement such as we may suppose provisionally for the stapes (the stapes, however, does not act as a true piston, as has just been explained), then its movement downwards would be about one-third of the stapedial movement, for its area here is three times as great —that is, about $\frac{25}{3}\mu$, but, since it bends, I estimate that the downward displacement of the basilar membrane, measured to the deepest point of its curvature, will be about 25μ.

Sir Thomas Wrightson has already dealt fully with the movement of the cilia of the hair cells. I propose to go over the same ground, in order that I may deal with their structure from an anatomist's point of view.

It will be mutually helpful to see how far my interpretations meet the needs of his theory. It will be most convenient to deal with a maximal movement of the basilar membrane, such as has been alluded to in connection with Fig. 9. Since we cannot observe such movements directly, we must infer them from a consideration of the fixation of parts, the quality of the material out of which these parts are framed, and the relationship of one part to another. The organ is far too complex to be analysed *en bloc ;* we must take up the various constituents—the basilar membrane, the arch pillars, Deiters' fibres, the reticular membrane, the tectorial membrane—one by one, and then see how far the properties of these several parts will affect the movements of the organ as a whole.

As an anatomist, my main aim is to obtain a rational explanation of these complicated parts. Helmholtz's theory does not tell us why the organ of Corti is provided with an intricate elastic framework of arch fibres, supporting (Deiters') fibres, and a reticular membrane. We get no clue to the division of the basilar membrane into subarcuate and striate zones, nor to the complexity of its fixation to internal and external spiral ligaments. No explanation of the internal and external spiral grooves is given, nor can we see, on his theory, the reason why the tectorial membrane should be fixed to the upper surface of Corti's organ and the cilia projecting within it. If we regard, as Sir Thomas Wrightson has done,[1] the scaffolding of the organ of Corti as a means for transforming the vertical movements of the basilar membrane into transverse frictional movements, whereby the cilia, embedded in the tectorial membrane, are laid under varying degrees of lateral stress and strain during the transverse frictional movements between the organ and its covering membrane, then much that was obscure becomes intelligible. We see why the organ should be furnished with elastic levers and an elastic scaffolding.

Up to this point I have followed the conventional interpretation of how the various phases of a sound wave as represented in Fig. 7 (p. 185) affects the stapes and basilar membrane. From this point onward I am to follow Sir Thomas Wrightson's interpretation. I had presumed, as others have done, that during phases IV and I (see Fig. 7, p. 185), the stapes was moving inwards and the basilar membrane was moving downwards, and that during phases II and III their movements were reversed; I had presumed that, during the sounding of a simple tone by a tuning fork, the stapes and basilar membrane repeated exactly the vibrating movements of the prongs of the fork.

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[1] Dr. Emile ter Kuile was the first to demonstrate clearly that the vertical movements of the membrana basilaris were converted into transverse movements between the plateau of the organ of Corti and the tectorial membrane. His description of the functional significance of the various parts of the organ of Corti is the best to be found in the literature of this subject. He believed that there was only one stimulus in each vibrational cycle—that produced during the descent of the membrana basilaris. (See Pflüger's "Archives," 1900, vol. lxxix, p. 146.

Sir Thomas Wrightson's demonstration compels us to give up that interpretation. A graphic synopsis of this new theory is given by Sir Thomas Wrightson at p. 134; to that diagrammatic representation (Plate VI) and to the part of his text where the various movements of the stapes, basilar membrane and organ of Corti are described, I would here refer the reader.

As regards the mechanism of the internal ear, the theories propounded by upholders of the Helmholtz theory and by Sir Thomas Wrightson are very different. According to the first, a single sound wave can produce but a single auditory stimulus—that stimulus arising at the end of phase III when the tips of the cilia hit against the tectorial membrane. According to this new theory, a single sound wave can and does produce four auditory stimuli—each of the four phases being distinctly separated from the others by a rest period or interval; the movement of each phase constitutes a stimulus. That is only one of the differences between the two theories; we shall note the others as we proceed. Meantime I propose to continue my survey of the organ of Corti and basilar membrane, to see which of those theories gives the most satisfactory explanation of the build and arrangement of the parts we shall encounter.

In Figs. 10, 11, 12 I have magnified the section of the organ of Corti represented in Fig. 13, and have at the same time stripped away all its parts, leaving only the middle and essential stratum of the basilar membrane with the arch *in situ*. The spiral ligaments, to which the middle stratum is attached, are shown, also the two parts of that stratum are indicated—the arcuate zone, elastic in nature and 65μ in width, and the striate zone, inelastic and 235μ in width. The thickness of the striate zone is less than 3μ; the arcuate is still thinner. In order to obtain a diagrammatic effect, I have supposed, in Fig. 11, that the inward movement of the stapes (in phase I), see Sir Thomas Wrightson's diagram, Plate VI, p. 134, has been sufficient to depress the basilar membrane to an extent of 10μ at its deepest part.[1] I have represented the basilar membrane as assuming the form of a curve—the deepest point of the curve being situated at or near the mid-point of the membrane. The depression of the membrane is attended, I presume, with two other effects: (1) the in-drawing or approximation of its points of attachment to the spiral ligaments—an effect to which Sir Thomas Wrightson has already directed attention. The exact amount of the approximation of the spiral points [Fig. 10 (*A–B*)] I cannot estimate with any degree of exactness, and therefore have not depicted it; but it must be considerable, because the structure of the spiral ligaments at the points of fixation indicates elastic properties of a high order. The other effect, produced by the downward curvature of the membrane, is its elongation; if we suppose that its points of fixation were immovable, there is, in such a movement as is shown in Fig. 10, an elongation of $1{\cdot}2\mu$, but the effect would fall mostly on the thin elastic arcuate zone; the part between *A* and *C* would stretch more readily and to a greater extent than the striate zone, *C–B*. We shall see that this may produce important effects on the movements of the organ of Corti. I am disposed to attach considerable importance to the elasticity of the arcuate zone; this zone is present in the basilar membranes of reptiles, birds, and mammals. In Fig. 10, I represent also the upward curvature which follows the outward movement of the stapes during phase III. The movements of the basilar membrane during the four phases of a vibrational cycle have been already depicted in Sir Thomas Wrightson's diagram.

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[1] I made a model—an enlargement of 600 diameters of the actual parts. I used the following materials: elastic threads, cotton threads, and thin cardboard. The movements and their effects were studied and measured on this model. The diagrams on Figs. 10, 11, 12, are made from the model.—A. K.

In Fig. 11, I carry the process of anatomical analysis a stage further. The arch is added to the membrane; attached to the head-plates of the arch two hair cells are shown, one of the inner row and the first of the three outer rows. We want particularly to see what movements take place in the apex of the arch and in the hair cells attached to its head-plates when the basilar membrane is set in motion. The two pillars are of about equal thickness—between 3 and 4μ; they have a fibrous structure and give the impression of having the degree of resistance of a fine hair. The inner is—at the point of the cochlea shown in Fig. 13—48μ long; the outer 72μ. The height of the arch is 44μ; its base is formed by the arcuate zone, 65μ in width. The foot-plate of the outer pillar is firmly planted to the inner end of the striate zone, which binds it to the external spiral ligament. The inner foot-plate is planted on the outer end of the internal spiral ligament. As they meet at the apex of the arch the pillars thicken—their

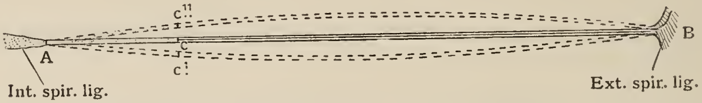

Fig. 10.—Diagrammatic representation of the movements of the basilar membrane. *A–C.* Subarcuate part, *C–B* striate part.

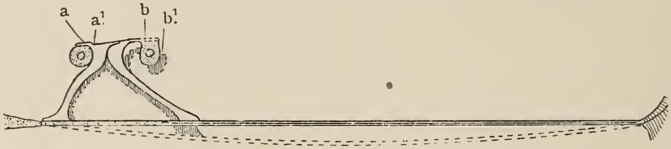

Fig. 11.—Movements of the same with arch attached. Movement of arch in phase I.

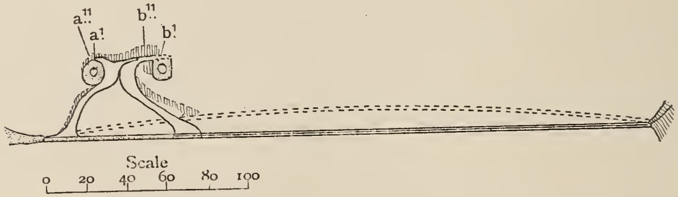

Fig. 12.—Movements of the arch and membrane during phase III. The scale shows measurement in microns.

combined thickness being 11μ. They are evidently jointed at the apex of the arch; but I have never observed a cleft representing an open joint; they must move on each other very stiffly.

Movements of the arched pillars and attached hair cells.—How far will the movements of the membrane be affected by the presence of the arch? I presume they will be very little affected. In Figs. 11, 12 I attempt to represent the motions of the arch in a movement similar in extent to that shown in Fig. 10. During such a movement the arch is rotated so that its apex turns downwards and outwards to an extent of nearly 4μ [1]; the inner and outer hair cells do not move exactly as the apex; the movements of the inner cell are 3μ—more outward than downward, while the outer, also about 3μ in amount, are more down than out.[2] The axis on which the arch turns is represented by a point on the internal spiral ligament, just internal to the inner foot-plate and near the site at which the nerve fibres perforate the internal spiral ligament. The inner pillar represents—approximately—the radius of the curve in which the apex of the arch moves. Since the arch strides the yielding elastic part of the basilar membrane, its span must widen as the membrane descends during phase I. The expansion at its base I estimate to be a little over 1μ, but even such a minute movement may have its effect on the hair cells and in the stimulation of their cilia.

In phase II (see Figs. 11, 12) the arch returns to the equatorial position, and the width of its span is reduced to the resting amount. In phase III the movements of the arch are peculiar (Fig. 12); the apex of the arch ascends upwards and slightly inwards, but towards the end of the movement, when the base of the arch is expanding, the inward movement ceases, and the apex comes to rest about 2μ above the equatorial position. The movement of the hair cells is upward and inward—the inward direction being more in the inner cell and the upward more in the outer. It is to be observed that during phases II and III the direction in which the hair cells move does not alter; the general trend for both these phases is upward and inward. At the end of phase IV the arch and hair cells return to the resting position. The movement of the arch and of the hair cells is the same, as regards direction, during phases II and III, but in phase II the span of the arch is contracting, in phase III it is expanding.

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[1] These measurements are inferred from movements in a model—enlarged 600 diameters above the natural size of the parts.

[2] So far as I know, Sir Thomas Wrightson and the writer were the first to try to estimate the movements of Corti's arch. Short of direct observation on the living cochlea, there can be no finality in our respective estimates.

The influence of the remaining elements of the organ of Corti.—In Fig. 13 I have added the remaining parts to the organ of Corti and then sought to show the effect of their addition on the movements of the basilar membrane. These remaining parts are five in number: (1) the fibres of Deiters and the cells by which these fibres are formed; (2) the reticular membrane formed out of the head-plates of Deiters' fibres; (3) the outer supporting group of cells; (4) the inner supporting group of cells; (5) two hair cells representing the second and third rows of the outer series of hair cells.

The fibres of Deiters, as seen in such a section of the organ of Corti as is depicted in Fig. 13, are three in number. They are of the same nature as the arch fibres, but more slender. They represent an essential part of the skeleton or scaffolding of the organ. Their lower ends are fixed to the striate part of the basilar membrane; they ascend obliquely upwards and inwards; they reach the upper surface of the organ external to the three corresponding rows of outer hair cells; like the pillars of the arch, when they reach the surface they expand into a head-plate or phalanx, which forms a delicate jointed armour on the upper surface of the organ; this surface plating is the reticular membrane. The upper ends of the hair cells, each carrying a series of about 15 cilia (reduced for diagrammatic effect in Fig. 13 to one), project through apertures formed between the joints of the reticular membrane. In these apertures the upper ends of the hair cells are securely fixed (see Fig. 15). Their cilia project above the level of the reticular membrane.

At the outer side, the organ of Corti is completed by a group of cells packed closely together and well filled with protoplasm. In Fig. 13 only the thin, resistant, elastic envelopes of the cells are depicted. Collectively their envelopes form a network of trabeculæ or fibres which have a downward and inward trend as they pass to be fixed to the striate part of the basilar membrane. The fibres are designed to prevent the outer supporting cells from being thrust in an outward direction. The surface of the outer supporting groups is covered by a thin membrane, which represents a continuation of the reticular membrane.

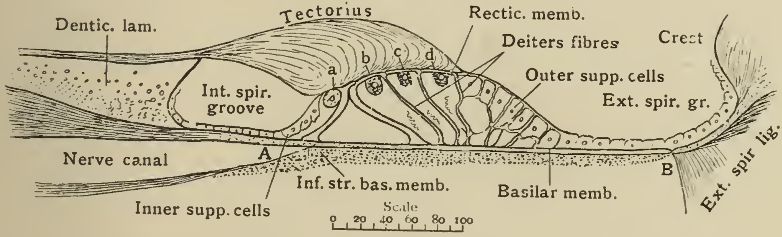

Fig. 13.—Diagrammatic section across the organ of Corti to show the more important elements. *a*, *b*, *c*, *d*, position of cilia in the zero position. The scale is in microns.

The inner supporting group of cells (Fig. 13) is much less in size and strength than the outer group. It, too, is covered by a thin resistant membrane.

Before I attempt to describe the movements of the organ as a whole, it is necessary to direct attention to certain spaces in its interior, which are filled by fluid (Fig. 22). The presence of such fluid spaces must have a distinct bearing on the changes in shape to which the organ will be subjected as the basilar membrane rises and falls. The space between the pillars of the arch is almost entirely occupied by fluid (Fig. 22); this tunnel space extends beyond the arch outwards to spaces between the upper ends of Deiters' fibres where the hair cells are situated. It also extends to the spaces round the inner hair cells. The presence of such fluid spaces will permit the organ to change its shape readily as the curvature of the basilar membrane alters.

It will be seen from Fig. 13 that the organ, or, to be more exact, the plateau of the organ, of Corti extends over two-thirds of the basilar membrane. Its depth or thickness is 58μ and is supported by an elaborate skeletal system of stiff elastic fibres, showing a definite and constant architectural arrangement. In Fig. 23 (p. 235) it will be seen that the plateau extends to four-fifths of the width of the basilar membrane near its commencement in the fenestral or basal region of the cochlea, but is confined to the inner half of the membrane—near its termination in the apical region of the cochlea.

The displacement movements of the ciliary plateau of the organ of Corti.—At first I was led to believe that the presence of a scaffolding like that which supports the plateau would alter the curvature of the displacement movements of the basilar membrane. Dr. ter Kuile was also led to draw a similar inference. But further experiments with an enlarged model led me to see that, with or without a scaffolding attached to it, a weight applied near the mid point of the basilar membrane always gave the maximum degree of displacement. Further, a weight attached to the basilar membrane at the junction of its middle and outer fourth always gave the maximum outward movement—the movement which gives a displacement outwards of the whole plateau when the membrane descends below or ascends above its resting position. The result of the transverse pull of the subarcuate zone is to increase the degree of transverse movement of the cilia-carrying plateau.

In my model I found, when the mid point of the curvature of the basilar membrane represented a downward or upward displacement of 12μ above or below the resting or zero position, that in each phase the cilia were moved in an oblique direction—outwards and downwards or inwards and upwards—to an extent which varied between 2 and 3μ. I do not think that a movement to the extent of 12μ ever occurs in the normal actions of the basilar membrane. We will not be far from the truth if we presume that the actual movement of the ciliary plateau never exceeds 1μ during a single phase.

The curvature of the basilar membrane alters at every phase; it is flat, concave, and convex in turn. The plateau must share in these alterations of form. In the downward displacement in phase I the parts of the organ immediately attached to the basilar membrane tend to open out, the parts on the ciliary plateau of the organ to be compressed. We see why the upper or tectorial surface of the organ is coated by a delicate jointed armour—the reticular membrane—in the meshes of which the brims of the hair cells are set. The plates come together as the basilar membrane descends and open out as it ascends. We see why the organ is supported by the delicate framework of Deiters' fibres. We see why there should be fluid spaces in the centre of the organ and why there are buttresses of supporting cells at either side of the plateau. There must be, too, an alteration in the curvature of the plateau in the upward and downward movements—curvatures which follow those of the basilar membrane. It is also clear to anyone who will examine the sections shown in Fig. 23 (p. 235) that these plateau curvatures must be more marked in the basal part of the cochlea, where the organ extends well beyond the central point of the basilar membrane, than in the special region, where the organ scarcely extends beyond the central point.

The functional significance of the arch pillars.—Sir Thomas Wrightson has treated the arch pillars (rods of Corti) as bent levers. In that I think he is right; but they certainly have a further significance to the anatomist. There can be no doubt they are modified—specialised—fibres of Deiters. Later, we shall have occasion to examine the organ of Corti in the bird (see Fig. 20), in which only Deiters' fibres are present, but in the reptilian ear (see Fig. 20) we can see certain Deiters' fibres—situated over the junction of the arcuate and striate zones—beginning to assume the arch form. The alteration is taking place just over the junction of the yielding and rigid zones of the basilar membrane. We see too, from the arrangement of parts, that the mobility of the reptilian basilar membrane (and organ of Corti) is greater in the reptilian than in the avian ear; the presence of an arch is associated with a greater degree of mobility. The mobility is still greater in the mammalian ear, and with that mobility the arch—spanning the elastic zone—becomes well defined. The arch is essentially an adaptation to facilitate displacement; it makes the organ of Corti sensitive to the slightest of displacing forces.

Thus in the displacement theory as elaborated by Sir Thomas Wrightson we have a satisfactory explanation of the structural conformation of the organ of Corti; whereas those parts are, for the greater part, unexplained in the theory of von Helmholtz. Dr. Emile ter Kuile (see footnote, p. 195) recognised in 1900 that the structural arrangement of the organ of Corti could be explained only on the basis of a displacement theory.

Importance of the tectorial membrane.—In the previous paragraphs I have been trying to build up a working picture of the organ of Corti. There is an essential part I have still to add—the tectorial membrane or tectorius. It is to the organ of Corti what a trigger is to a gun; it is the agent by which the cilia are moved and auditory stimuli produced. Its relationship to the organ of Corti is depicted in Fig. 13, and it will be seen that its movements must be correlated with those of the organ. Between the upper or reticular surface of the plateau and the under surface of the tectorius is a narrow space occupied by a fluid film. By interaction between the tectorius and upper surface of Corti's plateau the cilia are stimulated. The physical characters of the tectorius, its attachments and mechanism, become matters of the very first importance in any inquiry of this kind. Anyone who consults the numerous papers which give descriptions of the tectorial membrane will be puzzled by the various accounts which have been published of its shape, size, and structure. Those who have made a study of the ear know the difficulties of preserving its delicate parts in the position they occupied and in the form they possessed during life. The bone which surrounds the cochlea is extremely dense; before the cochlea can be cut into thin sections for examination under the microscope, the bone has to be dissolved away by the use of acids; in the process of staining and clarifying the sections, reagents have to be employed which distort and contract the more delicate parts. The tectorial membrane is one of the most delicate, and it undergoes a very remarkable degree of contraction and distortion in the preparation necessary for microscopical examination—as much as a petal does when dried in the sun. We owe our present knowledge of its true appearance and shape to Professor Hardesty.[1] His researches were carried out on the cochlea of young pigs; in such animals the cochlea can be extracted easily, the bone broken away, and the tectorial membrane examined in its fresh and unchanged state. We can safely transpose Hardesty's observations to the human ear, for in so far as the structure and mechanism of the cochlea are concerned man holds no advantage over other mammals.

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[1] Dr. Irving Hardesty, "The Nature of the Tectorial Membrane and its Probable *Rôle* in Hearing," *Amer. Journ. Anat.*, 1908, vol. viii, 109.

In Fig. 13 I have represented what I believe to be the true shape and relationships of the tectorius; the aspect presented is that which is seen when a section is made across the cochlear passage. In such a section we see the organ or plateau of Corti cut across with the tectorius—also cut across—forming a cap over the organ. The under surface of the tectorius is moulded to the upper surface of the organ, so that the cilia of the hair cells are apparently not only in contact with it, but project into it. There have been much doubt and much discussion as to whether or not the tectorius is fixed to the organ or whether it floats free. Anyone wishing to know the different opinions which have been expressed will find them in Professor Hardesty's paper just cited. For my part, I have no doubt at all; a minute examination of all microscopic sections of the cochlea I have at my disposal convinces me that it is fixed at both the outer and inner border of Corti's plateau or organ as shown in Fig. 13. But these two bonds are different in nature. The outer margin of the tectorius is formed by an exceedingly thin membrane which becomes continuous with the cuticular covering of the supporting cells on the outer side of Corti's plateau or papilla—just beyond the outer hair cells. This adherent membrane is not only exceedingly delicate, but is slightly folded, showing that it is loose to allow a certain amount of movement. The inner bond of the tectorius fastens it to the surface of the inner supporting cells. This attachment is firm and close; when the tectorius is detached from the organ, the internal point of fixation is seen to be marked by a thickening in the lower margin of the former—first observed by Hensen and known as Hensen's knot or stripe. Between these outer and inner bonds the under surface of the tectorius is free; the upper surface of the plateau to which it is opposed is covered by the delicate jointed reticular membrane. Between the opposed surface is a film of fluid—representing the film of oil which separates an axle from its bearing. We cannot understand the structure and relationship of the opposed tectorial and reticular surface unless we suppose side to side or transverse movements occur between them—the movement which is to stimulate the hair cells and evoke auditory impulses.

There is another important attachment of the tectorius; its main point of fixation—the base from which it derives its main support—is formed by the upper surface of the denticulate lamina (Fig. 13). It will be remembered that Sir William Bowman, when he discovered the lamina, could make no guess as to its use; Corti had already seen it and found that it gave attachment to the basal stalk of the tectorius. The tectorius begins on the lamina as a cuticle, which presently, as it passes outwards, becomes differentiated into an upper and lower layer; as these layers leave the denticulate lamina and spring inwards they are seen to break up into sprays of the most minute fibrillæ. Kolmer estimated that these were not more than $0{\cdot}25\mu$ in diameter. The pattern formed by these minute but apparently elastic threads may be seen in Hardesty's illustrations. The fibrillæ bend downwards from the upper to the lower surface of the tectorius and run some little way on that surface before terminating. The under surface of the tectorius is thus a felt work formed out of the woven, intermingled terminations of the fibrillæ. Thus the framework of the tectorius is made up of exceedingly delicate elastic threads; the interstices of the tectorius are filled by a semi-fluid, jelly-like substance. It is "inconceivably delicate and flexible" (Hardesty). It has the specific gravity of the endolymph surrounding and supporting it.

As seen in section (Fig. 13) the upper surface of the tectorius is strongly convex; the highest point of the convexity is situated always over the arch in the organ of Corti—the arch apparently representing the most flexible or extensible part of that organ. The lower surface of the tectorius is subdivided into an outer zone, resting on the plateau and hair cells—its ciliary surface—and an inner zone bridging the inner spiral groove—its free surface (Fig. 13). Of more importance from a mechanical point of view is the inner or attached margin—the stalk by which the tectorius is fixed to the upper surface of the denticulate lamina. No one can survey the appearance and structure of the tectorius—when such a section as that represented in Fig. 13 is examined—without being convinced that the tectorius is set like a spring on the denticulate lamina—a spring always in a state of tension—tending to lift itself from the upper surface of the organ. The structure, shape, and setting of the denticulate lamina are in keeping with such a view. The lamina is composed of a dense felt work of fibres running into toothlike processes under the attachment of the stalk of the tectorius; its upper outer angle forms a projecting elastic spring board for the tectorius; the deeper stratum of the lamina is an open sponge work.

We can only interpret these physical characters of the lamina and tectorius by supposing that in all its movements the tectorius remains in a state of tension. In every sense the tectorius is comparable with the lens of the eye.

With the addition of the tectorius we have thus before us (Fig. 13) a completed picture of the physical parts of the organ of Corti. We see that it is most delicately balanced on three sets of attachments. It is set on a triple arrangement of elastic strings; its lower inner angle is fixed to the elastic tissues of the internal spiral ligament, of which tissues the subarcuate (elastic) part of the basilar membrane may be regarded as an intrinsic part; its lower and outer angle is fixed by the pectinate fibres of the basilar membrane to the strong elastic and resisting structures of the external spiral ligament; its upper or ciliary surface is suspended from—or at least attached to—the denticulate lamina by the tectorius. The organ is suspended in and forms part of the column of fluid which is set into a to and fro motion by the excursions of the stapes. The exact character of the movements of the organ must be determined by its triple attachment to the walls of the cochlear passage. One point is clear—the organ will swing freely and easily with the column of fluid set in motion by the stapes.

It will present by its elasticity a resistance to the inward movement of the stapes; by its recoil it will aid the outward movement of the stapes. Its elasticity makes us certain that it will shadow or follow the stapes in all movements.

One other observation I must add here. If a section across both cochlear passages be examined—the upper or vestibular and lower or tympanic (Fig. 9), it will be seen that all the structures connected with the organ of Corti are designed to meet or resist rises of pressure in the upper passage; they are less designed or adapted to resist pressures arising in the lower passage. At its inner and outer attachment, the basilar membrane is mainly continued into the lining membranes of the upper—not the lower—passage. The supporting fibres of the organ are designed to withstand pressure applied to it from above—not from below. The tectorius is set so as to offer some degree of resistance to pressure exercised in a downward direction. In brief, the organ of Corti is so set as to offer some resistance to the inward stroke of the stapes; it offers less resistance to the outward stroke. If Sir Thomas Wrightson's theory is true, then we have a complete explanation of all these facts.

The ciliary cleft.—When we come to a final analysis of the motions of the organ of Corti and the production of auditory stimuli, we have to fix our attention on one small part of the organ—merely the ciliary cleft lying between its upper surface and the lower surface of the tectorius. In Fig. 14 I give a diagrammatic representation of what I conceive to be the movements which occur in this cleft during the four phases of a vibrational cycle. Into this cleft project the cilia of the four rows of hair cells; only four of these cells are shown in Fig. 14, and only one of the fifteen cilia provided to each cell is represented. The tips of the cilia project into the under surface of the tectorius, their lower ends are implanted within the hair cells. The brim of each cell is tightly fixed in an aperture of the reticular membrane. Now in phase I we have seen that the upper surface of the organ is carried in a downward and outward direction. The lower surface of the tectorius also moves, for it is bound to the organ of Corti, but, being hinged to the denticulate lamina and moving on a different axis from that of the organ, it moves down and also inwards, carrying with it the tips of the cilia. The total result of

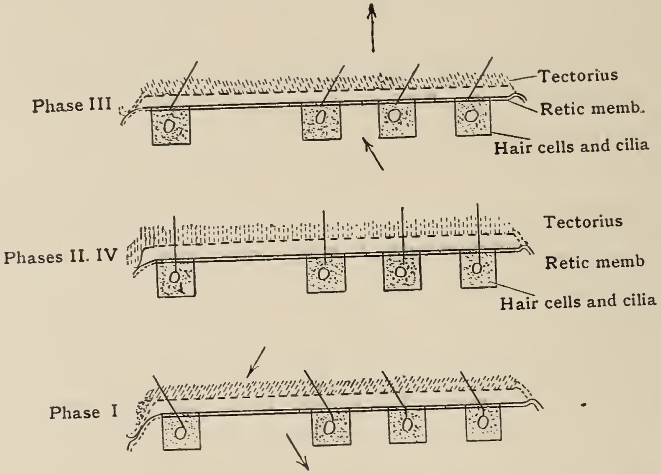


Fig. 14.—Cleft between Tectorius and Reticular Membrane. The arrows indicate the directions of motion. Four hair cells, with single cilia, are shown. Phases II and IV—the equatorial or resting position at the end of these phases. Phases I and III—at end of descent, phase (I), at end of ascent (III).

the motion in phase I is to bend the cilia inwards, to the spectator's left—the cilia are subjected to a sudden tension, their bases going with the hair cells, their tips with the tectorius (Fig. 14).

In phase II these movements are reversed and the organ returns to the resting position; at the commencement of phase II the motion of the cilia is reversed, producing a stimulus. At the end of phase II the cilia are in the position they occupied at the beginning of phase I (see Fig. 14).

In phase III the upper surface of the organ is moving in an upward and inward direction, carrying with it the bodies of the hair cells; the lower surface of the tectorius moves upwards and slightly outwards, carrying with it the tips of the cilia; the cilia during phase III are bent in an outward direction—exactly the same direction they were bending during phase II. In phase IV the movements of the organ and tectorius are reversed; the cilia begin to bend inwards; at the end of phase IV the parts have again returned to the equatorial or resting position.

Now at only two points in the completed cycle do reversals in the movement of the cilia occur—namely, at the beginnings of phase II and of phase IV. If we believe that only a reversal in the motion of the cilia can give rise to an auditory impulse, then each sound vibration produces only two stimuli—each of them at the point where the conventional tracing of a sound wave forms the apex of a crest or bottom of a trough. Helmholtz proceeded on the belief that an impulse arose only at the end of the upward movement of the basilar membrane—corresponding with the end of phase III, as interpreted by Sir Thomas Wrightson.

The nature of auditory stimuli.—In all our modern speculations regarding the mechanism of hearing there are certain beliefs we are all prepared to accept as true. These are: (1) The hair cells are the receivers or end stations in which auditory stimuli arise or are produced. (2) The ciliary processes are the levers or handles by which force or energy is conveyed to the hair cells. (3) Each separate application of mechanical force so conveyed gives rise to an excitement or molecular change in the cell. (4) This change is reflected along the nerve fibre which commences in or round that cell. The change so reflected along the nerve passes as a nerve message to the auditory centres in the brain. (5) Each separate application of force—whether by the bending of the ciliary processes or merely by altering the tension at their roots—will constitute a stimulus; but between each two applications there must be a definite interval of time; the force must also be applied above a certain rate per unit of time.

Sir Thomas Wrightson has shown that each vibrational cycle of sound is broken up into four phases when its motion reaches the basilar membrane; in each phase there is a transference of energy; each transference is separated from the rest by a distinct interval of equal degree; in each phase there is thus a stimulus, The mere reversal of the ciliary movement at the beginning of phases II and IV does not constitute a stimulus; the reversal of movement merely signifies that there was a stationary period, separating the stimulating or energy transferring periods which precede and follow the reversal of the ciliary movement. At the beginning of phases I and III there is no reversal of the ciliary movement, but these phases are separated by an interval when there is no movement. Thus the auditory nerve messages which pass into the brain may be represented by a series of dashes—the length of each dash representing the amount of energy transferred at each phase, separated by spaces—each space representing the interval in which there is no transference of energy by the ciliary processes. The length of the dashes represents the intensity or loudness; the number of spaces or intervals between the dashes stand for the pitch. The brain is supplied, just as a telegraph operator is, with all the data necessary to unravel the constituent elements of a complete message. We may also presume that a sudden acceleration in the movement of the ciliary process, or a sudden slowing, would count as the beginning of a new stimulus.

The hair cells and ciliary processes.—We cannot hope to experiment directly on a hair cell; it lies beyond the limits of the unaided eye. There are, however, certain sources of indirect evidence to which we may appeal. There is in the first place the actual structural appearance of hair cells. In Fig. 15 is represented a drawing by Retzius of the hair cells of the human cochlea when the upper surface of the organ of Corti is examined under a high magnification. As thus seen, each cell is oval in outline; the inner hair cells are compressed so that the long axis of their oval outline lies along the axis of the organ; the outer are compressed so that the axis lies across the organ. The surface of each cell is set in a framework formed by the reticular membrane. There are twelve to fifteen cilia for each cell arranged in a crescentic line across the oval surface, which measures 8–10μ in the long axis of the oval. Each cilia is about 6μ long and less than a micron ($\frac{1}{50000}$ inch) in diameter. The body of the hair cell is embedded in the organ of Corti; its neck or brim is encircled by a mesh of the reticular membrane. The depth of the cell, as seen in profile, varies from 20 to 40μ.

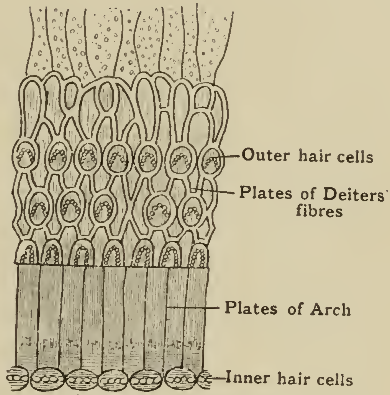


Fig. 15.—The Hair Cells and Reticular Membrane viewed from above (Retzius).

If then we apply to the movements of the organ of Corti and the cilia implanted on it, Sir Thomas Wrightson's interpretation—we see that in each vibrational cycle of the organ—corresponding with the vibrational cycle of a sound wave—there are four periods of motion separated by short intervals of rest. In each cycle there are four expenditures of energy separated by brief intervals of rest. Each separated expenditure of frictional energy represents a stimulus; each vibrational cycle gives rise to four stimuli, one at each "crossing-point" or "zero point," one at each trough and crest.

In any theory of hearing, one basal fact has to be taken into consideration. Why is it that a pitch of less than fifteen vibrations per second or of more than 15,000 is inaudible—is outside the compass of the ear? On von Helmholtz's theory this fact can be explained by supposing that there are no resonators for such notes. Why should they be absent? There is another possible explanation. The expenditure of energy to evoke a minimal stimulus must be almost infinitesimal, but there must be a minimal limit which falls below the amount of energy required. Is it not probable that, when the vibrational rate falls below fifteen per second the ciliary movements occur so slowly that the energy evoked is not sufficient to give rise to a stimulus? On the other hand, when the vibrational rate becomes excessive the movements of the cilia must become so slight that again the expenditure falls below the minimal requirements. It seems to me that the limitations of the scale of audibility can be explained as well—or even better—on Sir Thomas Wrightson's theory than on that of von Helmholtz. If it is true that a very low note or a very high one, inaudible when sounded softly, becomes audible when sounded loudly, then the explanation is to be found in Sir Thomas Wrightson's theory—not in that of von Helmholtz.

The evolution of the cochlea.—The theoretical consideration which I have just postulated rest, to a certain extent, on observed facts. It is necessary to allude to these facts because they help us to understand the nature and mechanism of the cochlea. Although our knowledge of the ear is far from complete, yet it is much fuller than it was when Helmholtz applied his genius to the mechanism of hearing. We know now for certain that all air breathing vertebrate animals—and man must be included in this group—have arisen from vertebrate forms which lived and carried on their respiration in water. To an animal living entirely in water an apparatus for perceiving vibrations of sound as we know them would be of little use; the ear which a fish requires is one which is sensitive to vibrations produced in and by water in motion. Hence it is that we find the first rudiment of the cochlea in Amphibia, the lowest of air breathing vertebrates. In the frog (see Fig. 16) the cochlea is represented by the minute recessus basilaris. The blind end of the recess is formed by a vibrating or basilar membrane; the hair cells are placed not on the basilar membrane—as in man and other animals—but on one side of the recess. The hair cells are covered by a tectorial membrane which is affected by the vibrations of the basilar membrane. The vibrations of the basilar membrane are conveyed to the cilia by the tectorial membrane. The rudimentary cochlea of the frog is not a new structure; it has been evolved out of a part of the elaborate vibratory system of the fish's ear or labyrinth.

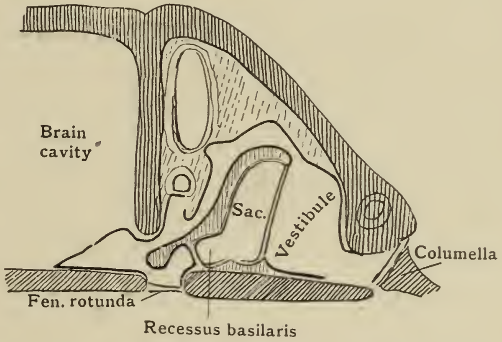


Fig. 16.—Diagram of the inner ear of the Frog to show the rudimentary cochlea or basilar recess (after Spencer Harrison).

In the fish the ciliary system of the labyrinth subserves a much more important function than the perception of vibratory motions in the water. The cilia set in the fluid of a fish's labyrinth are loaded at the tips, and hence come under the action of gravity; if a fish turns partly on its right side, then certain groups of cilia in the labyrinth also are tilted to the right under the weight of their loads, and this movement gives rise to a change in the hair cells and a stimulus to the brain, which results in a muscular movement tending to bring the fish back to its normal position. The important fact for us is that a motion of the cilia in one direction gives rise to a stimulus; the movement in another direction to another stimulus. Now it was from a group of ciliated cells possessing such properties as those just described that the cochlea of air breathing vertebrates was evolved. We therefore expect the auditory cilia to give rise to stimuli in a manner similar to the ancestral cells from which they were modified. But they have been changed in one respect. The cilia which react to gravity are loaded; the load acts as the immediate agent in bending the cilia and thus producing the energy which gives rise to a stimulus. Now with the evolution of the cochlea the load placed on the cilia became the tectorial membrane, but in place of being balanced on their tips and supported by them it became hinged to the wall of the cochlea by one margin, its lower surface resting on the upper surface of the organ of Corti with the cilia penetrating it. In place of being heavy and therefore subject to gravity, it became of the same density as the fluid of the cochlea.

Displacement versus Resonator Theory.

The aim I had in view as I wrote the foregoing pages was to build up a working picture of the machine which has the power of converting sound vibrations into nerve impulses.

At Sir Thomas Wrightson's instigation I approached the organ of Corti as one seeking to discover the use of its various parts and how they work together to produce a definite end. There is, however, another frame of mind in which one may make a study of the structure of the inner ear. Von Helmholtz, for instance, took up its investigation with a definite idea already formulated; he was convinced, as we have seen from a quotation cited on p. 172, that the only means by which sounds could be resolved into their primary tones was by a system of resonators, and that the ear, having such a power, must possess such a system. He selected first the fibres of the arch; then discarded them in favour of the fibres of the striated part of the basilar membrane. He never sought to explain the parts and mechanism of Corti's organ as a whole; he selected the parts which suited his theory and trusted to the future revealing the meaning of those parts he passed over without consideration.

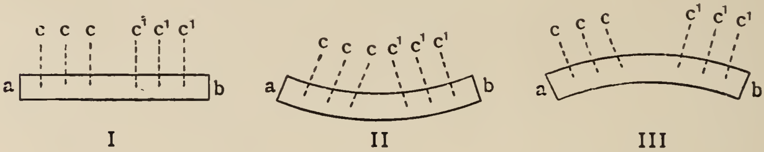
Sir Thomas Wrightson has also applied himself to the study of the mechanism of the ear in the same manner as von Helmholtz did. Forty years ago he demonstrated that if, in a tracing of a compound wave of sound, we suppose that a stimulus is produced not only at every crest and at every trough of that tracing but also at every point where the tracing crosses a zero or base line, then from such stimuli an analysis into primary tones could be produced by the brain. He was convinced that in the cochlea there must be a mechanism for producing a nerve stimulus at each of those four points in a wave of sound.

When I first began to study the structure of the cochlea on actual specimens, I soon became convinced, as has been the experience of all anatomists, that the basilar membrane was neither set nor framed to answer the purposes demanded of it by the Helmholtzian theory. The elaborate elastic framework of the organ of Corti, the structure and remarkable fixation of the basilar membrane, and the manner in which the tectorial membrane was applied to the upper surface of the organ—all these facts remained unexplained. But if we regard, as Sir Thomas Wrightson has done, the whole apparatus of the cochlea as the most delicate weighing machine ever invented—a balance for weighing the infinitesimal pressures of sound waves—then the structure and mechanism of the cochlea become intelligible. It is a balance which weighs and registers plus as well as minus pressures and displacements. The gradual widening of the basilar membrane as the cochlea is ascended from base to apex is to provide not a series of resonators, but a means of distributing pressure or displacement over an extensive area.

My real difficulty in accepting this new theory was due to a misinterpretation of the conventional tracing of a sound wave, and I think that a similar mistake is being made by most men who have sought to understand the mechanism of the cochlea. I had foolishly regarded the crests and troughs of such tracings as representations of maximal and minimal pressures—that the rise from trough to crest indicated a continued rise in pressure and the fall from crest to trough stood for a continued fall in pressure. I supposed that, as the sound wave ascended from the trough to the crest, the basilar membrane descended, and with the fall in the wave the basilar membrane ascended. It was easy to see in such an interpretation that a stimulus would be produced at each crest and trough, for at those points the ciliary movements were reversed. But I could not see how stimuli could be produced at the crossing points until it was made clear to me by Sir Thomas Wrightson that the crossing points in the tracing of a sound wave are points at which there are equally great changes in pressure and movement. At these zero points a new stimulus is produced. It is plain that distinct movements also start at the troughs and crests. Indeed it became evident and convincing that the demands which Sir Thomas Wrightson had formulated over forty years ago, but which have been neglected by medical men and physicists ever since, must be acceded to—that in every sound wave the organ of Corti passes through four separate movements, each of which gives rise to a nerve stimulus.

An abandoned explanation.—At one point of our inquiry—as Sir Thomas Wrightson is well aware—I was very much drawn to a mechanical method which gave the effects he was in search of—a mechanism which would give rise to four stimuli during a single vibrational cycle. That was before I had come to realise that such a vibrational cycle was divided into four separate periods of pressure. At that time it seemed to me essential, and indeed it seems so to me still, that the stimuli which are produced at the crossing points should be the same in nature and in degree as those produced at the crests and troughs. The four changes in pressure in a vibrational wave postulated by Sir Thomas Wrightson would give rise to four stimuli of the same nature and degree. The mechanism which had occurred to me is represented diagrammatically in Figs. 17 and 18, and it appealed to me because it seemed to give a fuller explanation of the structure of the organ of Corti than any other I had met with in literature. Six bristles are shown implanted vertically on a bar of indiarubber—arranged in two sets to represent the inner and outer hair cells (Fig. 17). The bar represents the basilar membrane and organ of Corti. The effects of bending the bar are shown; when the bar is bent downwards the tips of the bristles are approximated, when bent upwards they diverge. In Fig. 18 the free projecting parts of the bristles are represented as embedded in a jelly-like mass—this mass representing the tectorial membrane. The effects of bending the bar downwards and upwards are shown (Fig. 18). It is clear that during an excursional cycle the resistance offered by the jelly-like mass to the movements of the bristles alters four times. Clearly the arrangement in this artificial mechanism has a close resemblance to the parts which make up the completed organ of Corti.

Now from an anatomist's point of view such a conception of the mechanism of the organ of Corti has something to commend it, particularly when the organ of Corti of the bird and reptile are studied. We have to explain the presence of the arch in the organ of Corti. We have to explain why the hair cells are divided into two sets: an inner consisting of only one row, and an outer set of three rows. The apex of the arch is the dividing line between these two sets (see Fig. 22). The cells of the inner row are different from those of the outer row; their cilia have an outward inclination, like the pillar of the arch against which the inner hair cell is set; the cilia of the outer cells have an inclination inwards, like the outer pillar of the arch. The cilia, too, on the inner hair cells are set in a straight row, running parallel to the inner margin of the organ of Corti; on the outer hair cells the cilia are arranged in a horse-shoe line, with the toe of the shoe directed towards the outer margin of the organ of Corti



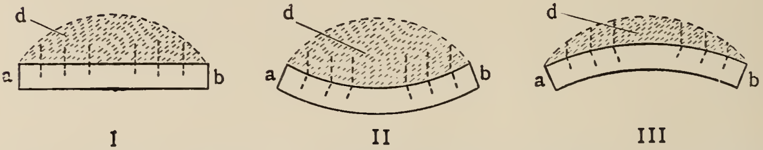


Fig. 17.—Bar of rubber with six bristles implanted vertically on it. I. In the zero or horizontal position; II. with the centre bent downwards; III. with centre bent upwards.

Fig. 18.—The same with the bristles embedded in a mass of jelly placed on the upper surface of the bar. The effects on the bristles when the bar is bent are represented.

(see Fig. 15). All these facts have to be explained. Now if we suppose the tectorius merely acts as a passive body for resisting the movements of the cilia, resisting their approximation and divergence, and that the essential motions of the organ of Corti are its bendings and unbendings as illustrated in Figs. 10, 11, and 12, and that the centre or axis at which these bendings occur is situated between the pillars of the arch, we obtain nearly a complete explanation of all the structural peculiarities of the organ. We see why its upper surface should be covered by a delicate, elastic jointed armour; we see why it should be strengthened by an elaborate system of elastic supports; we see why the tectorius should be an exquisitely sensitive flexible elastic body, and why over the apex of the arch—the centre of the bending surface of the organ—there are no hair cells and no cilia (see Fig. 22). The only difficulty is the one described in discussing what I believe to be the essential movement of the Corti plateau—namely, its movement in a transverse direction.

Appeal to Comparative Anatomy.

Now when we are in doubt as to the exact mechanism of any obscure structure in the human body there is always one source of evidence open to us—that of comparative anatomy. To help us in deciding as to what may be the exact manner in which the cochlea converts sound impulses into nerve stimuli I am to refer to the cochlea of the bird for the following reasons. There can be no doubt the ear of birds has an analytical power; many of them can sing and have, we must suppose, the power of appreciating song; they distinguish one call from another. Several kinds of birds imitate human speech; such imitation would be impossible unless their ear appreciated and distinguished the various modifications of tone combined in our speech. We must therefore presume an analytical power in the cochlea of the bird.

The ear of the bird is likely to give us a clue to the mechanism of the cochlea for the following reason. All the evidence at our disposal leads us to believe that birds and mammals have been derived from a common ancestry; they have become very different in appearance because they have specialised along totally different lines. We feel certain therefore that the ears of birds and of mammals are modifications of a common form and that, although they may differ greatly in detail of structure, yet the underlying principle on which they work must be the same. For that reason I am to devote a few paragraphs to the ear of the bird. Retzius has published excellent sections of the bird's ear.

In Fig. 19 I reproduce a section made across the ear of a sparrow; it corresponds exactly with the section across the human ear depicted in Fig. 8. In the case of the bird, a single bone—the columella—connects the drum with the oval window. While the outer end of the columella is fixed to the drum, its inner end expands into a foot-plate which is fixed into the margin of the oval window by a ligamentous membrane. The lower and hinder borders of the foot-plate are more tightly fixed in the window than the upper and anterior margin, not unlike the manner in which the stapes is attached in the fenestra ovalis of the mammaliam ear. The movements of the columella are more like those of a lever than of a piston; it is hinged to the lower margin of the oval window. Internal to the foot-plate (Fig. 19) is the cavity of the vestibule, filled with fluid. A horizontal partition is drawn across the floor of the vestibule, stretching from the lower margin of the oval window, which is occupied by the foot-plate, to the opposite or inner wall of the vestibule. The partition is seen to be made of three parts (see Fig. 19): (1) a plate of cartilage attached to the lower margin of the fenestra ovalis; (2) a thin membrane—the membrana basilaris; (3) another plate of cartilage (inner plate, Fig. 19) which is perforated by the auditory nerve-fibres. The basilar membrane is stretched from the one plate of cartilage to the other. Placed on the upper or vestibular surface of the membrane is the organ of Corti, forming a sickle-shaped stratum, on the surface of which are implanted numerous hair cells. Over the hair cells is the tectorial membrane (Fig. 19, *g*). As already said, the nerves reach the organ of Corti by perforating the inner plate of cartilage, which therefore represents—in part at least—the bony spiral lamina of the mammalian cochlea. The outer plate of cartilage represents—at least part of it does—the external spiral ligament. In Fig. 19, however, it will be noted that the middle passage (scala media) of the cochlea

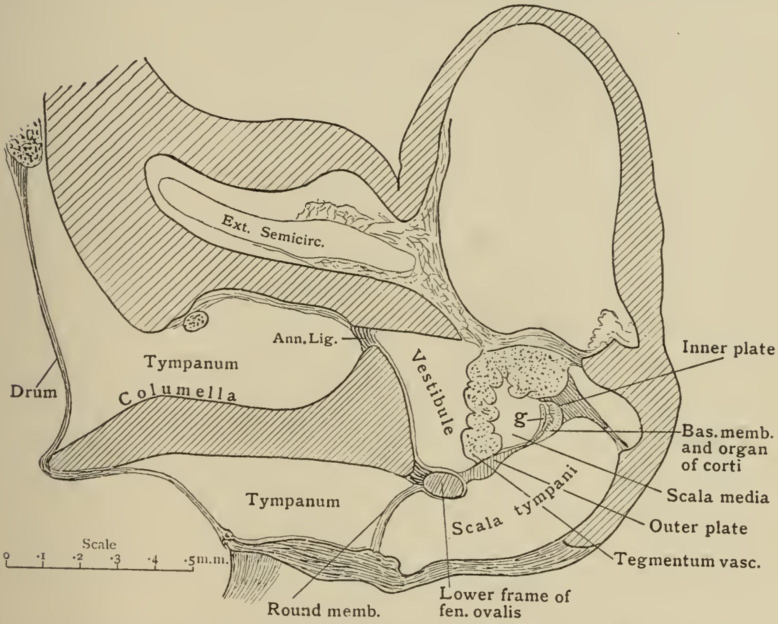


FIG. 19.—Section across the drum, columella, vestibule, and commencement of the basilar membrane of a sparrow.

is separated from the cavity of the vestibule by a thick folded membrane containing many blood vessels—the tegmentum vasculosum It represents a combination of Reissner's membrane and the vascular body (stria vascularis) of the mammalian ear.

The horizontal partition just described forms the floor of the vestibule and the roof of the lower or tympanic passage of the cochlea—at least the terminal part of that passage. The round window lies immediately below the oval window (see Fig. 19). It is closed by a strong but loose membrane which is placed between the lower end of the tympanic passage and the cavity of the middle ear or tympanum.

Now in considering the mechanism of the bird's ear we may omit from our calculations the movements of the tegmentum vasculosum (Fig. 19); it is a slack membrane and may be regarded for our present purposes as forming part of the fluid which fills the vestibule. When, then, the outer end of the columella is set into vibration by the drum, its foot-plate will carry the impulses of the drum to the fluid filling the vestibule. As in the mammalian ear, we may distinguish four phases in each vibrational cycle. In phase I the foot-plate, starting from its point of rest, moves or rotates inwards, displacing a minute quantity of the vestibular fluid. The vestibule has firm walls everywhere except that part of its floor formed by the basilar membrane. The membrane yields, displacing the fluid contents of the lower passage and forcing outwards the round membrane. In phase II the foot-plate returns to its starting point, and the basilar membrane and organ of Corti rise to their equatorial level. In phase III the outward excursion of the foot-plate continues, and the basilar membrane rises so as to become convex upwards; the round membrane is drawn in. In phase IV all these parts return to rest.

In Fig. 19 only the commencement of the basilar membrane is represented—the part situated in the floor of the vestibule. In the mammalian ear the membrane begins in a similar way and is drawn out into an ever-widening ribbon, about 35–40 mm. long, which reaches to the apex of the cochlea. In the bird the cochlea is short and straight, the basilar membrane and organ of Corti form a narrow strip only 4 or 5 mm. in length. The upper and lower cochlear passages are equally short; the commencement of the upper and termination of the lower passage are shown in Fig. 19. At the further end the two passages join at a wide helicotrema.

As represented in Fig. 19 the basilar membrane and organ of Corti are on too small a scale for demonstrating their movements and showing the manner in which the hair cells are stimulated. Hence in Fig. 20 I represent a section across the organ of Corti made about halfway along a bird's cochlea. In filling in some of the details of the section I have borrowed certain points from the splendid illustrations of Retzius. At the point shown the basilar membrane of the sparrow is 115μ in width; it is stretched between the edges of the two cartilaginous plates already mentioned—the inner conveying the nerves.

The edges or corners of the plates are composed of dense fibrous tissue and serve the same purposes as the internal and external spiral ligaments of the mammalian ear. Further, one notes, as the middle and essential stratum of the basilar membrane is traced into the projecting edges of the two plates, that its substance passes into the floor of the upper—not of the lower—passage just as we found to be the case in the mammalian ear. As in mammals, the basilar membrane is composed of two zones—an inner, structureless, thin, apparently elastic and yielding, and an outer or striate zone, composed of fibres. The fibres are less densely packed together than in the mammalian ear. The striate part forms about four-fifths of the width of the membrane; when stretched, one would expect the narrow, inner, structureless zone to yield most. The middle area of the membrane is strengthened by the addition of a lower stratum to its tympanic aspect.

The organ of Corti is represented by a complex stratum of cells. This stratum is set not only on the upper surface of the basilar membrane but also directly above the inner projecting shelf (Fig. 20). The thickness of this stratum over the inner shelf and above the point at which the auditory nerve fibres perforate (Fig. 20) is 25μ; as it passes outwards on the basilar membrane it becomes gradually reduced to a depth of 10μ. In the construction of this epithelial or sensory stratum we find essentially the same elements as in the organ of Corti of mammals. There are, in the first place, hair cells, but in place of there being only four rows set on a plateau, there may be as many as 30 or 40 rows to be seen cut across on a single section. The cells are set closely together; they commence on the elevation over the inner shelf and extend outwards over the inner three-fourths of the basilar membrane; they are not present over the outer quarter. A vertical pressure applied at the junction of the third with the outer fourth gives the maximum lateral movement of ciliary processes. The framework of the stratum in which the hair cells are set is made up of exceedingly delicate elastic fibres—of the

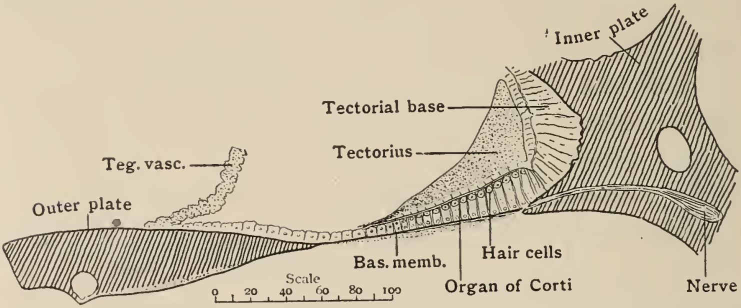


FIG. 20.—Section across the organ of Corti of a sparrow. Scale of enlargement indicated on the figure is in microns.

same nature as Deiters' fibres in the mammalian organ of Corti. These supporting fibres are fixed by their footplates to the basilar membrane (Fig. 20); their upper ends expand and form a delicate jointed reticular membrane in which the necks or brim of the hair cells are set. The interstices of the supporting fibres are filled with cells. The fibres of the auditory nerve pass through the framework to end in fine terminals round the hair cells. Where the hair cells cease over the outer fourth of the membrane the epithelial stratum becomes a one-celled layer, but the envelopes of the cells are thick and apparently of a resistant nature. The stratum in which the hair cells are set is thus a firmly knit, elastic structure; when bent it will tend to spring back to its resting form when the displacing force is withdrawn. The specialisations seen in the mammalian ear are absent: the inner and outer spiral grooves, the arched pillars, the outer and inner supporting groups of cells are not present. A tectorial membrane is present (Fig. 20). It is of the same elusive, delicate nature as in the mammalian ear; it crumples up and becomes distorted in all methods by which the ear can be prepared for microscopic examination. As it contracts under hardening reagents it also distorts the organ of Corti to which it was closely applied during life; hence the difficulties encountered by anatomists in interpreting the functional significance of the various parts of the bird's ear. In Fig. 20 I have restored the tectorial membrane to the form which my studies have led me to believe must be regarded as its true one. It is attached to Corti's stratum both at the outer and at the inner border of the hair cells. The cilia, about 4μ long, very stout at their bases and pointed at their tips, project into the lower surface of the tectorius. As in mammals, the tectorius is hinged to the inner wall of the cochlea—above the level of the hair cells. The method of hingeing is peculiar; in place of a long flexible stalk there is an extensive union by a wide base. The peculiarly elongated cells on the inner wall of the cochlea, to which its base is hafted, represent the cells of the upper surface of the denticulate lamina, but in the bird that lamina is so tilted that what is its upper surface in the human ear here becomes turned outwards. It is plain that this method of fixing the base or stalk of the tectorius gives it the properties of a spring—one which offers a certain degree of resistance to disturbing forces and a power of quickly recovering its position of rest.

We are now in a position to estimate the effects which will follow the columellar movements in the bird's ear. The thinnest and most flexible part of the basilar membrane lies in its outer fourth; both the epithelial stratum and the tectorial membrane increase in thickness and in power of resistance as we pass to the inner border of the membrane. When the foot-plate of the columella moves inwards from its zero position in the fenestra ovalis to its inward limit, the basilar membrane will be bent downwards, the maximum curvature being near its centre. We have to remember the thin inner elastic zone of the membrane which will permit this curvature to take place more easily. We shall have a slight rotational movement of the hair cells outwards and downwards—not unlike the movement of the upper surface of the organ of Corti in the mammalian ear. But it is also clear that the tectorial membrane is so shaped and hafted that it can share in this movement to a much lesser degree than the epithelial stratum on the basilar membrane. A frictional movement, very limited in extent, must occur between the tectorial and epithelial strata—a friction or strain which will bend the cilia of the hair cells inwards, towards the spectator's right in Fig. 20. It is unnecessary to recite the changes which occur in the remaining three phases of a vibrational cycle; it will be apparent that they give rise to the same ciliary movements as in the mammalian ear.

In the bird's ear there are no arch pillars, and no differentiation between outer and inner hair cells. Instead of only four cells on a single section—as in the mammalian ear—there are 20 or 30. How are we to explain these facts? It seems to me that the ear of birds is designed to work with very minute displacement volumes; the movements of the basilar membrane and of the ciliary processes must be of slight extent. The stimulus, if slight, affects in each section of the cochlea a great number of sensory hair cells, and is thus magnified. The bird's cochlea is a machine for gathering and weighing much minuter displacement volumes than is the case in the mammalian ear. In the mammalian ear all the evolutionary tendencies have been towards a free stapedial displacement, more ample movements of the basilar membrane and of the ciliary processes. The arch pillars have been introduced to serve as levers; the mammalian organ is restricted in width, and the sensory cells are reduced to four, as seen on a transverse section.

It was when I first came to examine the bird's cochlea that I was drawn to adopt the explanation represented in Figs. 17 and 18, but the mechanism which we have worked out for the mammalian ear gives much the more satisfactory explanation of the form and structure of the parts. Indeed in the bird, as in the mammal, the mechanism seen in the organ of Corti and tectorial membrane is, as Sir Thomas Wrightson has pointed out—one for converting the vertical movements of the basilar membrane into horizontal movements between the organ of Corti and the tectorial membrane.

Von Helmholtz's theory helps us to a most imperfect interpretation of the ear of the bird; on the other hand, the theory put forward by Sir Thomas Wrightson—if it does not give us a full and complete clue to every item in its structure—serves this purpose to a much higher degree than any other I know of. I shall return again to the arrangement of the hair cells on a long narrow ribbon in mammals and on a short wide one in birds.

The Organ of Corti in the Alligator.

For our present purpose an examination of the cochlea of the alligator will prove instructive. In many parts of its anatomy the alligator shows relationships to mammals; in other parts to birds. The cochlea, as may be seen from a section across it (Fig. 21)—a modification of an illustration given by Retzius), is an intermediate form; in some respects it resembles the avian type, in others it is mammalian. The tectorial membrane and the cushion to which it is attached are of the avian rather than of the mammalian type. We see in the stratum of sensory or hair cells the beginnings of certain definite mammalian features. As in the mammalian ear, the hair cells are of two kinds —inner and outer. But in place of only one row of inner cells there are four or five rows, and in place of three rows of outer cells there are about 20 rows. In birds there is only one kind—resembling the outer hair cells of mammals. Retzius has pointed out that the basilar membrane of the alligator, like that of birds and mammals, is made up of two zones—a narrow, inner, structureless, elastic zone, and a wide, outer, striate zone. The junction of the two zones lies under the point of separa-

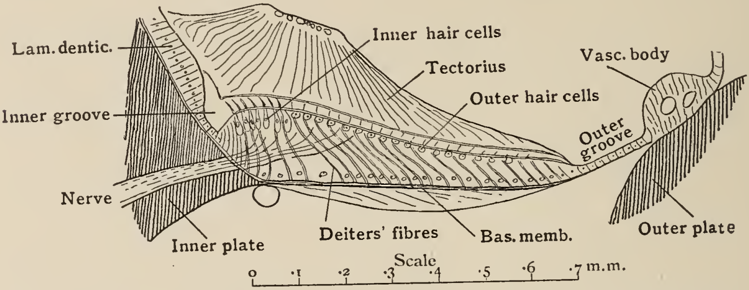


FIG. 21.—A section across the organ of Corti of the alligator (after Retzius).

tion between the two kinds of hair cells. Further, it will be noted that Deiters' fibres are long and well marked in the sensory layer (Fig. 21). Those which support the cells of the outer kind ascend obliquely upwards and inwards. Those between the inner cells and set on the inner elastic zone of the basilar membrane are more vertical. We have here a clear foreshadowing of the arch of Corti—the arch pillars; the apex of that arch lies between the inner and outer sets of hair cells in mammals. Further, in Fig. 21 it will be seen that the internal spiral groove, the external spiral groove, and vascular body are clearly indicated in the cochlea of the alligator. The part of the sensory stratum in which the hair cells are placed has become raised up into a plateau—the plateau which becomes so definitely marked in the mammalian ear. The structural arrangement of the alligator's cochlea becomes evident if we suppose the mechanism is the same as we have presumed for birds or mammals.

The most difficult feature to explain is the presence of two kinds of hair cells. They are clearly related to the arch pillars; the apex of the arch is always the line of demarcation between outer and inner cells. It is difficult to believe that these two forms of hair cells fulfil exactly similar functions. Their difference must be due to each kind being exposed to a different kind of tension or friction—which would be the case if the elastic zone, which lies beneath the inner hair cells—extended and contracted in depression and elevation of the basilar membrane.

The Organ of Corti in the Rabbit.

In discussing the structure and mechanism of the mammalian cochlea we confined our attention to the human organ. It will be as well to broaden the basis on which we build by an appeal to some other mammalian form. I select the rabbit for three reasons: (1) because Retzius has published most excellent drawings of its labyrinth (Fig. 22); (2) because its sense of hearing is very keen; (3) because we obtain confirmation of the conclusions we have already reached concerning the mechanism of the cochlea. I direct attention to the thinness of the elastic (subarcuate) zone of the basilar membrane—the zone which forms the floor of the arch—and to the thickness and strength of the striate zone; it is reinforced by a second or deeper stratum. The inner hair cell is set on the axis of the inner pillar; the three outer cells on the axis of the outer pillar and fibres of Deiters. The outer supporting cushion of cells bulges outwards from the side of Corti's plateau. The reticular membrane is strong. We know that we are dealing with a machine which is sensitive to the slightest sounds. The inner elastic zone, under the arch, must yield to the smallest depression or elevation of the basilar membrane, caused by the stapedial movements. The plateau of Corti is high above the basilar membrane, and its rotational movements, as the basilar membrane rises and falls, will thus be relatively large. The basilar membrane, because of the thinness of its

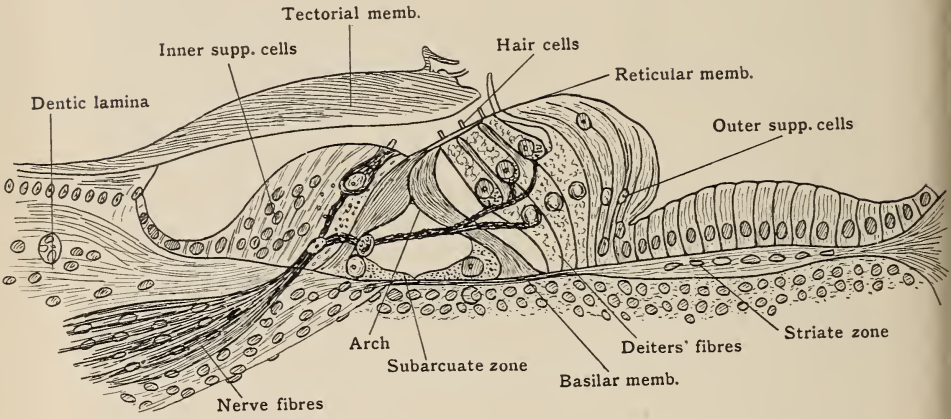


FIG. 22.—Section across the organ of Corti of the rabbit, from the middle turn of the cochlea (Retzius). The tectorius is represented as torn from what should be considered to be its natural position.

elastic zone, will be most sensitive to variations in pressure and yield a relatively large ciliary movement—conditions necessary to give sensitiveness of hearing. It is also plain that the movements of the outer hair cells will not be identical with the inner ones. The Wrightsonian theory gives us an explanation of all these features; that of Helmholtz does not.

Further Consideration of von Helmholtz's Theory.

Having thus described the anatomical basis on which Sir Thomas Wrightson's theory must be tested, I now return to a further consideration of that of von Helmholtz. The one point in the structure of the ear which was satisfactorily explained by von Helmholtz was the gradual widening of the basilar membrane from base to apex of the cochlea; the widening is certainly comparable to the ratio which regulates the dimensions of strings in a harp or piano.

Sir Thomas Wrightson has taken this feature of the cochlea into consideration and decided, on good grounds I think, that the widening of the basilar membrane as it ascends the cochlea has no relationship to a resonating function, but is an adaptation for a totally different purpose—that of distributing the stapedial displacements over the whole surface of the basilar membrane. I want again to go over this feature and to deal with it from an anatomist's point of view. Whatever explanation we offer for the gradual widening of the basilar membrane in man must hold true for mammal, bird, and reptile, for in each of these it widens as it passes towards the apex of the cochlea. In the reptile and the bird the membrane is only about 5 mm. in length; in man it varies from 35 to 40 mm. The first question we have to answer is: Why is the mammalian cochlea drawn out into so long and narrow a ribbon? The hair cells in the bird are almost as numerous as in the mammal; in the mammal the organ of Corti is drawn out so that the hair cells are arranged in three or four long rows; in the bird they are arranged in thirty or forty short rows. We find a difficulty in explaining these two opposite arrangements of hair cells, if we accept von Helmholtz's theory. Let us suppose that the part of the basilar membrane exposed in Fig. 22 (the rabbit's ear) and that in Fig. 20 (the sparrow's ear) respond to the same note. In the rabbit only four cells are stimulated; in the bird forty cells are stimulated. The bird should, therefore, hear the note much louder—have a keener sense of hearing and a less degree of discriminating one tone from another—than the rabbit. As a matter of observation, this does not appear to be the case; so far as we know, the one holds no advantage over the other in either of these respects. If we view the matter as comparative anatomists, the widening of the basilar membrane is evidently not connected with a resonating function, as von Helmholtz thought, but is an adaptation to some other end.

The power of the basilar membrane to resist pressure diminishes as the membrane is followed from base to apex of the cochlea.—To appreciate the true significance of the elongation of the basilar membrane, and its gradual increase in width from base to apex of the cochlea, one must examine a series of sections made transversely across at various parts of its course. The sections shown in Fig. 23 are drawn from a series of excellent preparations from the human ear by Dr. J. S. Fraser and Dr. J. K. M. Dickie. From these sections they constructed an enlarged model. I have to thank them for kindly giving me the loan of the original sections for the purposes of this research, and I also take this opportunity of thanking Dr. Fraser for his personal assistance. The position of the various sections in the length of the basilar membrane is shown in Fig. 23, the lowest being 7 mm. from its commencement in the vestibule; the highest 33 mm. from its commencement and about 2 mm. from its termination. Its length

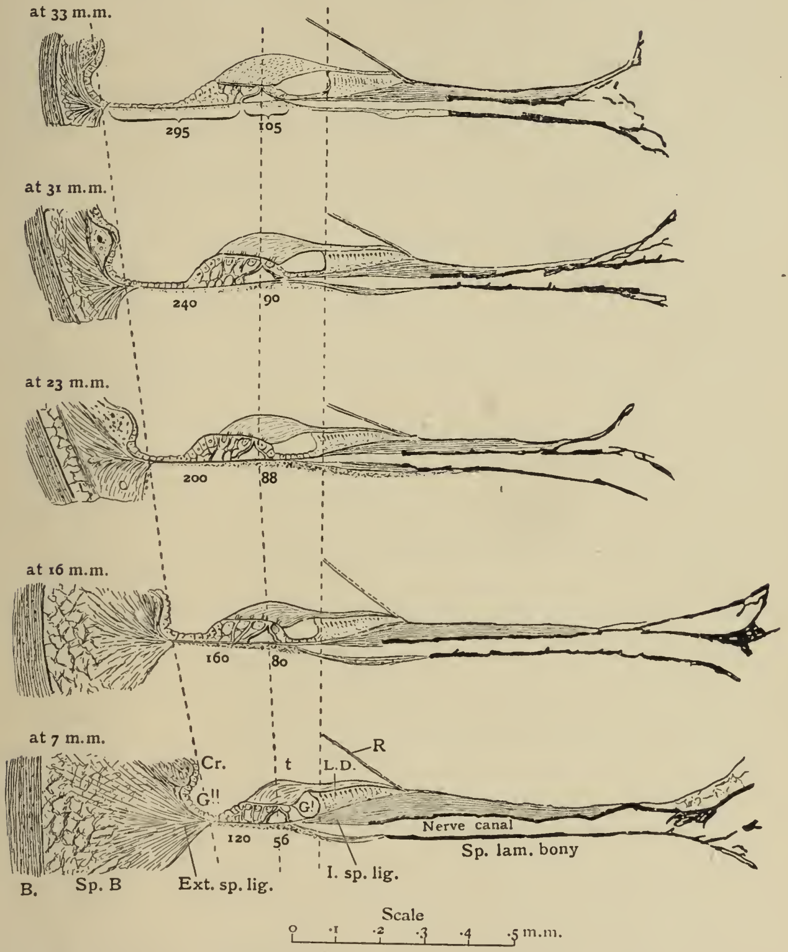


FIG. 23.—A series of drawings of the human cochlea from preparations made by Dr. J. S. Fraser and Dr. J. K. M. Dickie. The distance of each section from the commencement of the basilar membrane in the base of the cochlea is given with each drawing. The measurements placed immediately under the basilar membrane in each drawing refer to the widths of the subarcuate and striate zones.

was estimated by measurements made along its longest—the convex—border. In Fig. 23 the scale of enlargement is shown. When the series is examined it is seen that the widening of the basilar membrane is only one of a series of changes which takes place as the cochlea is ascended.

(1) Both parts of the membrane—striate and subarcuate—increase at an almost similar ratio.

(2) The outer spiral ligament, as Bowman noted and as Dr. Albert Gray has emphasised, decreases in bulk and strength as the basilar membrane widens.

(3) The internal spiral ligament keeps the external company in this respect.

(4) The internal spiral groove—the width between the denticulate lamina and the organ of Corti—widens with the basilar membrane.

(5) So does the stalk of the tectorius which bridges the internal groove.

(6) The fibres which form the pillars of the arch lengthen and their span widens as the basilar membrane widens.

(7) The tectorial cap increases in width and depth or thickness as the cochlea is ascended.

(8) So does the width of the plateau of Corti's organ.

(9) The bony plate of the spiral lamina decreases as the basilar membrane widens, but the ratio of the decrease is not regular.

(10) As the cochlea is ascended the outer edge of the bony plate is more and more withdrawn from under the denticulate lamina.

(11) There is one section of the basilar membrane which increases steadily and gradually in width, from beginning to end of the cochlea—the part lying external to the organ of Corti, the uncovered part, between the organ and the external spiral ligament.

(12) Further, the basal parts are the more richly supplied with nerves ; as the helicotrema is approached the supply becomes much poorer. One who believes in the truth of von Helmholtz's theory will have a difficulty in explaining all these facts. If we are dealing with a system of resonators, why should there be this complex series of

changes—the increased length of strings being only one of them—as we ascend from base to apex of the cochlea? They are features which are not incidental to the human ear; they are true of all forms in which there is an auditory mechanism of the cochlear type.

The primary utility of the sense of hearing.—As von Helmholtz pursued his investigations he had in mind the human power of discriminating sounds and the human capacity to enjoy music. The comparative anatomist comes to the study of the cochlea with another thought in his mind—the primary utility of hearing. In the rabbit or bird safety depends on their being able to hear the slightest disturbance as well as being able to discriminate one sound from another. Now we can see two principles on which a cochlea might be designed. We might design it so that its movements are very slight, but these slight movements would affect a large number of hair cells as in the bird; or we might design it so that the movements become of greater amplitude and affect a smaller number of hair cells, as in the mammal. The more we limit the area of the basilar membrane the smaller are the displacement volumes needed to give rise to stimuli, as in birds; the larger we make the area of the basilar membrane the larger are the displacement volumes needed to produce effective stimuli, as in mammals.

The explanation of the structural modification seen in the various segments of the organ of Corti.—If we look at the series of sections depicted in Fig. 23 as suspension or swing bridges, it is very difficult to believe that they are designed to meet equal degrees of pressure. The lowest bridge with the shortest span is provided with massive, strong lateral supports; the topmost has more than twice the span, but has the weakest lateral support. If we set up an artificial series of such bridges—built according to scale out of string to represent the striate zone, a rubber band to represent the subarcuate zone, and a framework of thin cardboard with elastic jointing to represent the organ of Corti—we can form a comparative estimate of the results of loading such a series with an equal weight. In such a model, the initial tension of the elastic segment being the same in all, the bridge yields to the greatest extent—not when the weight is applied to the mid point of the span, but at a point which lies a little way internal to the mid point. When the same weight is suspended in this series of models, which represents the sections shown in Fig. 23, the result is the following: beginning with the lowest in the series—the one with the narrowest span—the central point descended 30 mm. (the model was × 1500 diameters); in the second, 43 mm.; in the third, 52 mm.; in the fourth, 65 mm.; in the fifth, 72 mm. In the actual cochlea these would approximately represent movements of 2μ, 3μ, $3{\cdot}5\mu$, $4{\cdot}4\mu$, $4{\cdot}8\mu$. The bridges become more yielding with greater amplitudes of swing as we ascend from base to apex of the cochlea. It is very difficult to believe that those bridges are intended to be exposed to equal degrees of pressure; if they were, why should the short bridge with its small amount of leverage be supplied with the greatest lateral supports, and the longest span with the weakest? If, however, we suppose that only maximal displacements, caused by the most extreme of stapedial movements, actually reach the apical region of the cochlea, then we have an explanation of the series of bridges graduated in span and strength. I do not see how the varying features of those basilar bridges can be explained if we regard the basilar membrane as a series of resonators.

There was another important feature which I noted while applying equal weights to the series of experimental models of the basilar membrane. It will be remembered that there are two zones in that membrane—an inner hyaline and apparently elastic, and an outer fibrous, inelastic. I found that the elastic zone was more stretched when the weight was applied to a point of the basilar membrane roughly corresponding to the junction of the outer and middle fourths. If the series of sections shown in Fig. 23 be examined it will be seen that the centre of the outer spiral groove lies nearly at this point; the thinnest point in the basilar membrane occurs where pressures give the maximum stretching of the elastic zone and the maximum lateral displacement of the organ of Corti with its plateau of hair cells. That is as it should be, if the theory advocated by Sir Thomas Wrightson be the true one; but the position of the external spiral groove is inexplicable on the theory that the basilar membrane is a resonator.

To explain these structural modifications of the basilar membrane and organ of Corti, I think it is necessary to presume that the Wrightsonian theory is true, and that the apical sections are designed for the reception of slow displacements of higher total pressure, and that the short basal bridges are designed to pass displacements of lower total pressure; the total pressure spoken of being the area of each section of the basilar membrane, multiplied by the unit mean pressure of each increment of the air wave as it passes in. From base to apex the cochlea is designed to deal with displacements which vary in amount and rapidity. That is essentially the conclusion which Prof. Max Meyer reached a good many years ago.

Sectional areas of the scalæ at various points of their course from base to apex of the cochlea.—In Fig. 24 is illustrated another adaptation of the cochlea for the distribution of the stapedial displacement—one which I investigated at the request of Sir Thomas Wrightson. In the upper part of that figure (*A*) the basilar membrane is represented to scale and drawn out straight, in place of being coiled. The measurements were taken from the sections and model of the ear I obtained from Dr. Fraser. The actual length of the convex border was a little less than I found in three other series of specimens ; if we take the accepted average length of 35 mm. we shall be very near the mark. The width represents measurements made between the inner foot-plate of the arch (included) and the outer spiral attachment. The relative dimensions of the arcuate and striate zones are indicated in Fig. 23. Below the spread out basilar membrane (*A*, Fig. 24) is placed a diagram to represent the sectional areas of the upper and lower passages of the cochlea. Broadly speaking, the sectional areas of the two passages—estimated by plotting their outlines on millimetre paper—diminish as the width of the membrane increases. Sir Thomas Wrightson has analysed the effect which the diminishing calibre of the vestibular passage produces on the column of fluid displaced by the stapes from the vestibule. That diminution is clearly a further adaptation to secure a wide and rapid distribution of the displacement column.

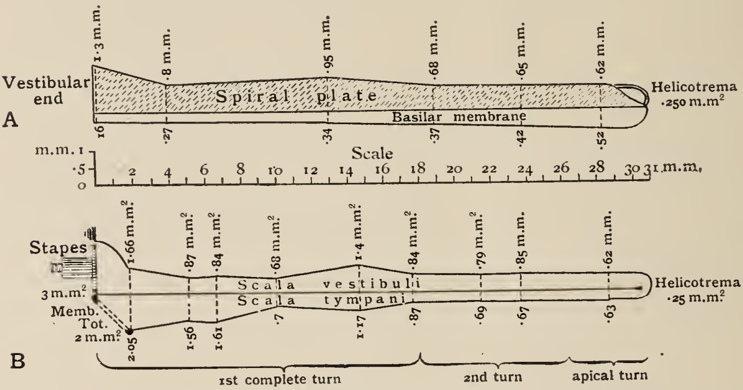


FIG. 24.—*A*. The dimensions and shape of the human basilar membrane and bony spiral lamina. *B*. Diagram of the sectional areas of the cochlear passages. (Drawn to scale.) In each case the actual measurements and scale of measurements are given.

Prof. Max Meyer[1] and several others who have investigated the cochlea in recent years have concluded

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[1] See references to recent literature, p. 254.

that this distributional mechanism of the cochlea will tend to confine displacements caused by vibrations of small amplitude to the basal part of the basilar membrane, while only waves of the greatest amplitude will reach the apical region. The poorer distribution of nerves to the apical part of the organ of Corti leads one to suspect it is of less functional importance than the basal and middle parts. There is no doubt, too, that early investigators presumed a much greater degree of stapedial displacement than actually exists. From what one knows of the passage of fluids along elastic flexible tubes—and the tympanic passage is partly of this nature, for the basilar membrane forms a segment—a minute one—of its wall—we may presume that the minimal displacement caused by the stapes would be so slight in amount that it would be dissipated —have passed into the tympanic passage—in the first few millimetres of the vestibular passage. The area of the basilar membrane affected, the number of hair cells stimulated, will therefore depend on the size of the displacement wave. There is experimental and clinical evidence to show that disease or destruction of the basal (fenestral) part of the cochlea produces deafness to high tones; disease or destruction of the apical (helicotremal) region result in deafness to tones of a low vibrational number. On von Helmholtz's theory such effects find an easy explanation; but it is also evident that on the displacement theory there is a full and satisfactory explanation.

The same distributional mechanisms is seen in the cochlea of reptile and bird.—In Fig. 23 I have depicted the series of modifications which occur in the mammalian organ of Corti using the human form as a type. In Fig. 25 I reproduce four drawings from Retzius to show that similar changes occur in the organ of Corti of the bird and reptile. We want to see whether the resonator or the displacement theory gives the more satisfactory explanation of their structural modification. In them the organ of Corti is only between

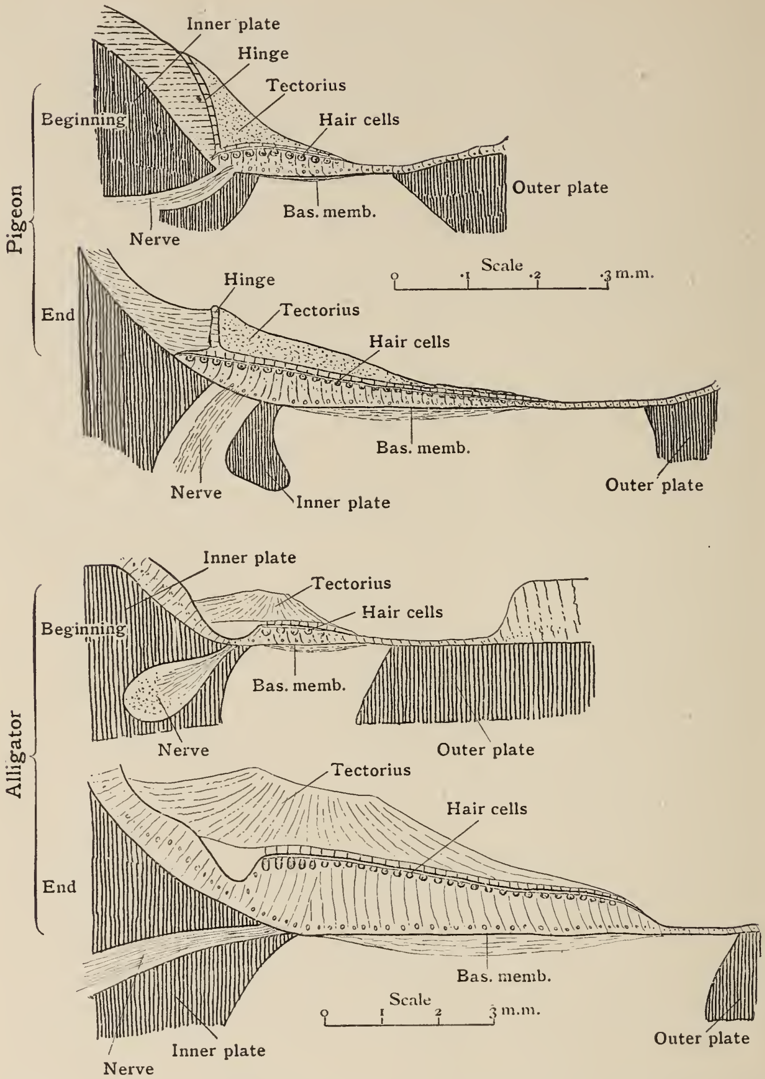

FIG. 25.—Section of the organ of Corti of a pigeon near its proximal (basal) end (Retzius). Section near its distal (apical) end (Retzius). Section of alligator's organ of Corti at basal end. At apical end (Retzius).

4 and 5 mm. long, but, as we have already seen (p. 225), it is crowded with hair cells. Taking the organ of Corti of the bird first—in this case a pigeon—it will be seen,

when sections across the beginning and end of the organ are compared, that the following differences are to be noted: (1) the basilar membrane near its beginning (Fig. 25) is 180μ wide; near its termination 500μ; at corresponding points the human basilar membrane is 176μ and 400μ. (2) At the beginning or basal part of the bird's cochlea the hair cells are few in number and gathered into a narrow area, half of them being situated above the inner shelf. (3) The tectorius is attached by a wide base to its cushion or denticulate lamina. Its lower margin or surface, which is in contact with the cilia, is less in extent than the fixed edge or surface. Near the termination of the bird's basilar membrane the hair cells are distributed over a wide area and are closely packed; the tectorius has a narrow attachment and a wide margin in contact with the cilia. It is clear that the parts as arranged at the commencement of the cochlea offer a much greater resistance to a displacing force than the structural arrangement at the end. In the bird, then, there is the same distributional mechanism as in the mammal—the same graduated series of modifications from its proximal to its distal end.

In Fig. 25 corresponding sections of the alligator's organ of Corti are represented, from original drawings by Retzius. Near its commencement the basilar membrane is 220μ wide; 800μ near its termination. The rows of hair cells near the commencement are few in number—one row of inner cells and four rows of outer. The grooves representing the internal and external spiral grooves of the human ear are narrow; the attachment of the tectorius to the inner wall of the passage is relatively close to the organ; the tectorius is small. Near the apical termination of the organ of Corti in the alligator there are six rows of inner hair cells and twenty rows of outer hair cells. The spiral grooves are wide, the attachment of the tectorius is removed some distance from the organ; its surface which covers the hair-cells is wide. Here again we meet with the same kind of structural modifications as in the mammalian and avian organs of Corti.

Significance of the elongation of the basilar membrane in the mammalian ear.—We must admit, I think, that the essential part of the organ of hearing—the cochlea—is built on the same plan and works on the same principle in mammals, birds, and reptiles. Why then is the field of cilia packed in an abbreviated triangle scarcely 5 mm. long in the bird and spread along an attenuated ribbon-like triangle in the mammal? The resonator theory can offer only an imperfect explanation. If we say the bird has a limited range of resonators and the mammal an extensive one, we make an assertion which is not confirmed by observation in living animals; we have no evidence which gives us ground to believe the range of the rabbit's ear is of wider compass than that of the pigeon. Nor can we explain why a set of resonators in the bird's ear is provided with twenty or thirty hair cells while a corresponding section in the rabbit has only four or five. If, however, we accept the displacement theory we do find a satisfactory explanation of these facts. The degree of structural similarity which underlies the organ of hearing in reptiles, birds and mammals assures us they are modifications or specialisations of a common form. Comparative anatomists are convinced that mammals, birds, and reptiles have been evolved from a common ancestry. It is clear that the bird has specialised in one direction, the mammal in another, and the reptile in one which is intermediate. We may well suppose that the bird's organ of Corti and cochlear passages are nearer the original than are the corresponding parts in mammals. In the bird the eye has become the chief sentinel sense; in mammals the ear, or ear and nose, is the chief watchdog of safety. We expect the mammalian ear to be a more sensitive organ than the bird's. What then is the functional direction in which the mammalian ear has specialised? It is in the direction of sensitiveness to displacement; in the bird the drum is connected with the cochlea by a single stiffly-set lever; in the mammal a mobile chain of bent levers has been introduced for this purpose. The structure of the organ of Corti in the bird gives the impression of stiffness; in the reptilian cochlea the organ of Corti begins to be raised into a plateau; the tectorius begins to lose its wide attachment to the denticulate lamina; there is some degree of adaptation for mobility. In the mammal this process has been carried much further; the plateau is narrow and raised; the tectorius is stalked. By stretching the basilar membrane into a narrow ever-widening ribbon means were found to make it capable of registering a great range of displacement volumes and yet be sensitive to all. For instance, the area of the basilar membrane in a pigeon is approximately 1·7 mm.^{2}; in man, it is 13 mm.^{2}; the first can deal with only minute displacement volumes, the latter with a wide range of displacement volumes. This capacity in the mammal can be obtained only by elongating and increasing the area of the basilar membrane. In place of a short, wide ciliary area being stimulated, as in the bird, it is a narrow, long area which is excited in mammals.

Irregularity in the sectional areas of the scalæ—There is another feature of the human ear which Sir Thomas Wrightson and I observed when investigating the calibre of the cochlear passages. In Fig. 24, *B*, it will be observed that the vestibular passage does not diminish continuously from vestibule to helicotrema; it diminishes during the first 10 mm., but beyond that limit it begins to dilate, continuing to do so for an extent of 5 mm., and then again begins to contract. The tympanic passage is more uniform in its rate of contraction, diminishing from helicotrema to the round window, but even in this passage too there is a reduction or constriction about 10 mm. from its lower end. These irregularities in the calibres of the cochlear passages are not accidental ; in Fig. 26 I reproduce the combined measurements we obtained from two specimens of human cochlea which were cut into sections in planes at right angles to each other. We had thus an opportunity of eliminating any accidental error in our estimates.

We again see the secondary dilatation of the vestibular passage. I have examined numerous metallic casts of the cavity of the inner ear and in all of them the secondary swelling on the vestibular passage can be observed. It is plain that a constriction and dilatation on the vestibular passage must have an influence on the wave or column displaced by the stapes.

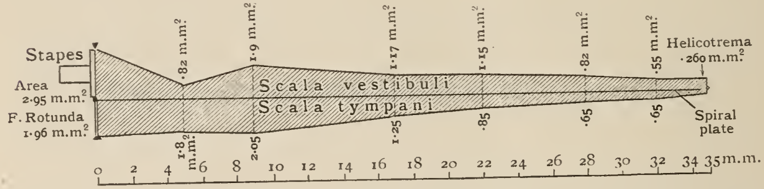

FIG. 26.—A diagram drawn to scale showing the length and calibre of the upper and lower cochlear passages in the human ear. The helicotrema, by which they communicate, is drawn to the same scale. The width of the passages represents their sectional areas.

The hair cells are not related to the fibres of the basilar membrane in the manner postulated by von Helmholtz.—I must now go back and take up a modification in the organ of Corti which I purposely omitted when dealing with its mechanism. As depicted in the diagrams (Figs. 4, 5 and 9) the organ of Corti is represented in transverse section—in a plane parallel to the fibres of the basilar membrane. I have led the reader to suppose that the depression and bending of the organ of Corti took place in the plane which is represented in these figures. If the resonator theory is true, all the hair cells seen in such a section should move with the vibrations of the underlying basilar strings. There is evidence that this cannot be the case. In Fig. 27, A, I show the upper surface of the tectorial membrane; its upper fibres do not run transversely across it, but obliquely; they are directed outwards but also apexwards—partly in the direction taken by the displacement column as it ascends the vestibular passage. In Fig. 27, *B*, is shown the upper surface of the organ of Corti; the outer hair cells are not arranged in transverse but in oblique rows, their direction being the same as the tectorial fibres. Lastly, the phalanges (Fig. 27, *C*) of the reticular membrane are similarly arranged. Each outer hair cell has its phalanx, supported at the end of a Deiters'

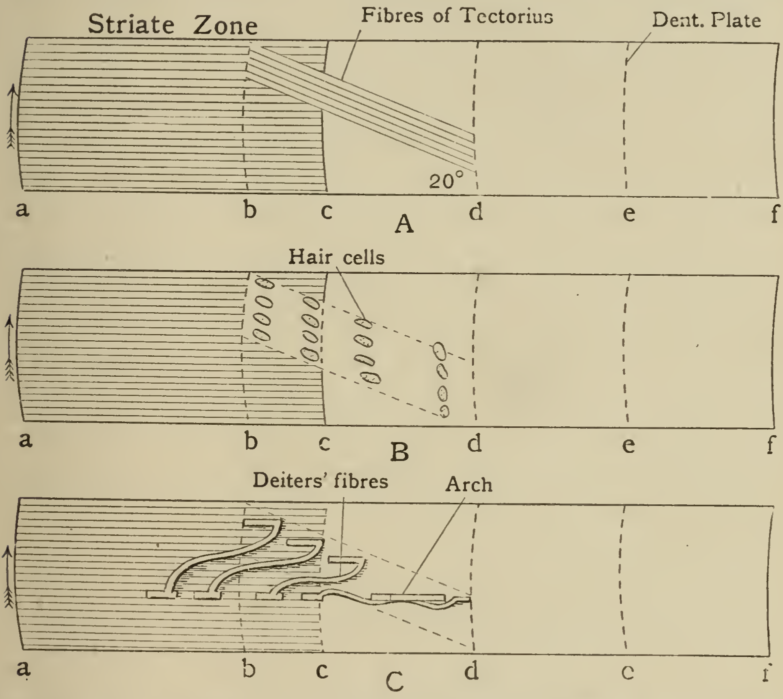

Fig. 27.—*A*. A segment of the basilar membrane showing the transverse arrangement of the pectinate fibres and obliquity of the tectorial fibres. *B*. The obliquity of the rows of hair cells. *C*. The bending of the outer fibres of Deiters towards the apex.

fibre. The fibre for the outermost hair cell does not arise from the basilar membrane immediately under that hair cell, but at some distance lower down the passage, nearer the base (Fig. 27, *C*). Similarly, the supporting fibres for the middle and inner hair cells are obliquely set, being bent towards the apex of the cochlea, thus bent in the direction taken by the displacement column. The fibres of the arch rise vertically to the plane of the basilar membrane. The fibres of the auditory nerve also turn towards the apex, as they approach the hair cells. A fibre may supply rows of cells extending over one-fourth of a turn. From all these facts one infers that the bending and depression of the tectorius and reticular membrane and hair cells do not take place at right angles to the direction of the displacement column, but are to a certain extent in the same direction—obliquely towards the apex. Such an arrangement of the supporting fibres increases the flexibility of the organ of Corti. In all these features we see obstacles to regarding the organ of Corti as a part of a resonator system, but all are in keeping with the displacement theory set forth by Sir Thomas Wrightson.

The fluid of the cochlea.—There is another matter which deserves our consideration. What is the tension of the fluid within the cavity of the inner ear ? How is the tension regulated ? How is the fluid secreted and absorbed ? The tension cannot be greater than that within the blood venules of the inner ear ; it cannot be greater than the venous pressure. The pressure would thus vary with the venous pressure ; we may infer that it would support a column of mercury 2 to 4 mm. high. There are no arterial pulsations in the fluid of the inner ear—not so long as that cavity is closed ; but when a fistula or opening is formed in its wall by disease, then pulsations do occur, but these produce no effect on the cochlea ; the movements they cause are too slow to stimulate the hair cells, but they do stimulate the cells of the semi-circular canals and thus disturb the balancing mechanism of the body.

There is another manner in which the tension may be regulated. The position at which the foot-plate of the stapes comes to rest is determined by two muscles which act on it—the tensor tympani and the stapedius. The former can press it inwards; the latter can draw it outwards. By their tonus these muscles exercise a constant effect on the stapes—balancing it. The tensor tympani could press the stapes inwards and raise the pressure within the ear; the stapedius could produce an opposite effect; between them they could regulate the pressure of the inner ear—within certain limits.

The helicotrema.—So long as the helicotrema is open a gradual rise or fall in the labyrinthine pressure cannot influence the position or tension of the basilar membrane. The helicotrema, the aperture between the two cochlear passages at the apex of the cochlea, is variable in size and shape. I have now examined six specimens; its shape is usually irregularly crescentic, its longest diameter being about $\frac{1}{2}$ mm., its area about 0·15 mm.^{2}, but it may be only 0·08 mm.^{2}, or it may go up to 0·2 mm.^{2}. It is markedly less in size than the terminal part of either passage.

Nature has also secured the safety of the basilar membrane against any sudden rise of pressure in the vestibule. A blow on the ear—an explosion—might force the foot-plate of the stapes so violently inwards that the displacement volume would rupture the basilar membrane. Nature has secured us against such an accident by binding the stapedial foot-plate of the oval window by a ligament of remarkable strength.

Everyone who has studied the mechanism of hearing has presumed that the walls of the inner ear are rigid and closed except at the two fenestræ. In that I think we are justified. It is true that blood and lymph vessels emerge from the cavity, but the stapedial vibrations are evidently insufficient to displace their contents. The main exit for the perilymph of the ear is situated at the termination of the lower or tympanic passage just above the round window. It serves simply as a minute additional round window.

Bone conduction of sound vibrations.—There remains one very important matter which must be considered because of the light it throws on the mechanism of hearing. We have been regarding the stapes as the main agent in producing the fluid displacements which stimulate the organ of Corti. There are on record authentic cases of men and women who have been able to hear after the foot-plate of the stapes has become immovably fixed in the oval window. So long as the organ of Corti is intact and the round window flaccid, hearing is still possible. There is another allied condition. Patients who have become partially deaf from destruction of the drum of the ear have their hearing improved when a slight resistance—such as a pellet of cotton wool—is applied to the stapes. When the movements of the stapes are hindered *hearing is improved.* When sounds are conducted to the inner ear by means of the bones of the skull, in people with normal hearing, the volume of sound is markedly increased if the movement of the stapes or drum is hindered. I do not think these conditions have been yet explained.

How are displacement volumes produced under direct bone conduction ? The total capacity of the cavity of the inner ear of man I estimate to be approximately 200 cubic millimetres ; 130 of these are contained in the main cavity, or vestibule, and semi-circular canals ; 70 are contained in the passages of the cochlea. I presume that, were the thick, exceedingly dense, and elastic bony walls of the inner ear completely closed, the fluid filling it would be subjected to a rise of pressure during the condensation phase of every sound wave; the pressure would fall in every rarefied phase. If the cavity, instead of being completely closed, had a flaccid window in it, then the rise and fall of pressure would be accompanied by a movement of that membrane. I presume that in the condensation phase of a sound wave a column will be displaced from the vestibule towards the round window; in the rarefied phase it will move back towards the vestibule. The basilar membrane will participate in all movements of the displacement column and give rise to stimulation of the hair cells. If, however, there are two windows in the inner ear, the oval one in the wall of the main chamber as well as the round window in the lower passage of the cochlea, part of the displacement column will escape by thrusting the stapes outwards; the part which thus escapes is ineffective so far as the basilar membrane is concerned. Fixation of the stapes prevents such an escape. We see, then, why hearing is improved, in cases of bone conduction, when the movement of the stapes is hindered. We also see how small must be the volume which gives an effective movement of the basilar membrane.

We have thus in direct bone conduction a means of discovering the actual volumes required to produce effective movements of the basilar membrane. I am certain that von Helmholtz greatly overestimated their size. He supposed that the length of the ligaments which bind the foot-plate of the stapes to the oval window might be regarded as indicative of the excursional movements of the stapes. The lengths of these ligaments represent the limits of stapedial movements—the limits of the movements produced, not by the drum of the ear, but by the two muscles which act on the foot-plate of the stapes. The actual figures given by von Helmholtz for the inward movement of the foot-plate in a complete excursion were 56 to 73μ; Politzer's estimate is 70μ; Burnett, on the other hand, who observed the vibrational movements directly, gives them as varying from 1 to 32μ. The main cavity of the inner ear contains 130 cubic mm. of fluid; how much is displaced when a sound wave of a known vibrational rate and amplitude passes through the temporal bone? If we knew that, we could estimate the actual displacements of the basilar membrane and the movements of the hair cells when such and such a note is sounded. I think it will be found that the effective stroke of the stapes is less than 25μ in even the loudest tones.

The Present Attitude towards the Resonator Theory.

It may be of some interest if I review, very briefly, the present attitude of medical men to the various theories of hearing which have been placed before them. I have found no record of anyone who has made a study of the structure of the ear and retained a belief in the truth of von Helmholtz's theory with one exception—Dr. Albert Gray[1*] of Glasgow. He proposes a modification of the resonator theory. All recent editions of text-books of physiology give the first place to the resonator theory. Professor McKendrick[2] gives it his unreserved support; Howell[3] is judicial—regarding the resonator theory as untenable on anatomical and also on some physiological grounds; Starling[4] supports the Helmholtz theory with reservations; Dr. K. L. Schaefer,[5] who may be regarded as representative of the most expert German opinion, is in favour of von Helmholtz with reservations; he is inclined to consider an explanation put forward by Prof. Ewald[6] as a possible alternative; Halliburton[7] is of opinion that the mechanism of hearing has not yet been satisfactorily explained; Stewart[8] is in favour of von Helmholtz, but does not accept the basilar membrane as a resonating mechanism.

Lately a considerable number of men have adopted the

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[*] See Bibliography, p. 254.

opinion that von Helmholtz's theory is true, but that it is the tectorial, not the basilar, membrane which serves as a resonator. I think Siebenmann[9] was the first to put forward this view; von Ebner favours it; it has been taken up and stoutly advocated in America by Shambough and Prentice. Kishi also regarded the tectorial membrane as a resonator.

Rinne (1865), Volliolini (1885), Rutherford[10] (1886) were of opinion that the basilar membrane vibrated as a whole; it simply repeated the vibrations of the drum, but the manner in which the basilar vibrations stimulated the hair cells and gave rise to auditory impulses they did not seek to explain. Hardesty, who regarded the tectorial membrane as free, looked upon it as vibrating as a whole, its vibrations stimulating the hair cells along the whole length of the organ.

Ewald [6] put forward the following explanation in 1899. He found that a narrow strip of elastic membrane, shaped and suspended as the basilar membrane is and placed in a box filled with fluid, is thrown into a complex system of waves when sound vibrations are transmitted to the fluid in which the membrane is immersed. The main pattern alters with the note; each sound produces its own pattern, and the hair cells are stimulated by that pattern just as the retina is stimulated by the picture focussed on it by the lens. Waller put forward a somewhat similar explanation in 1891.

Professor Max Meyer [11] is the leading advocate of another explanation of the mechanism of the cochlea. He accepts the mass displacement theory and supposes that the extent of the basilar membrane stimulated depends on the volume of the mass. Goebel [12] also upholds a somewhat similar explanation. He regards each wave of sound as giving rise to two stimuli—one at the crest and one at the trough. The only investigator who has attempted to analyse the movements of the various parts of the organ of Corti and explain the use of its various parts is Dr. ter Kuile.[13] He regarded the displacement of the basilar membrane and organ of Corti much in the same manner as Sir Thomas Wrightson does, but was of opinion that only one movement was effective in producing a stimulus —namely, the downward movement corresponding to the phases numbered IV and I.

It will thus be seen that the defects of von Helmholtz's theory have been recognised, but no explanation yet put forward is regarded as sufficiently satisfactory to take its place.

As I corrected the proofs of this Appendix my attention was directed to a work by Dr. Henry J. Watt[14] Lecturer on Psychology in the University of Glasgow. He approaches the problems of hearing from the psychologist's point of view, but gives a summary of the various theories of the mechanism of the ear. He, too, rejects Helmholtz's conception of resonators, and puts forward a displacement theory, one which may be regarded as a modification of ter Kuile's.

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[1] Dr. Albert Gray, *Journ. of Anat. and Physiology.* 1900. Vol. 34, p. 324.

[2] Prof. J. G. McKendrick, "Hearing." *Encyclopædia Britannica.* 11th Ed. 1910.

[3] Prof. W. H. Howell, *Text Book of Physiology.* 1913.

[4] Prof. E. H. Starling, *Principles of Human Physiology.* 1915.

[5] Dr. K. L. Schaefer, *Nagel's Handbuch der Physiologie des Menschen.* 1905. Vol. 3, p. 467.

[6] Prof. R. Ewald, *Pflüger's Archives.* 1899, Vol. 76, p. 147; 1903, Vol. 93, p. 485.

[7] Prof. W. D. Halliburton, *Handbook of Physiology.* 1915.

[8] Prof. G. N. Stewart, *A Manual of Physiology.* 1914.

[9] Dr. F. Siebenmann, *Bardeleben's Handbuch der Analomie des Menschen.* 1897.

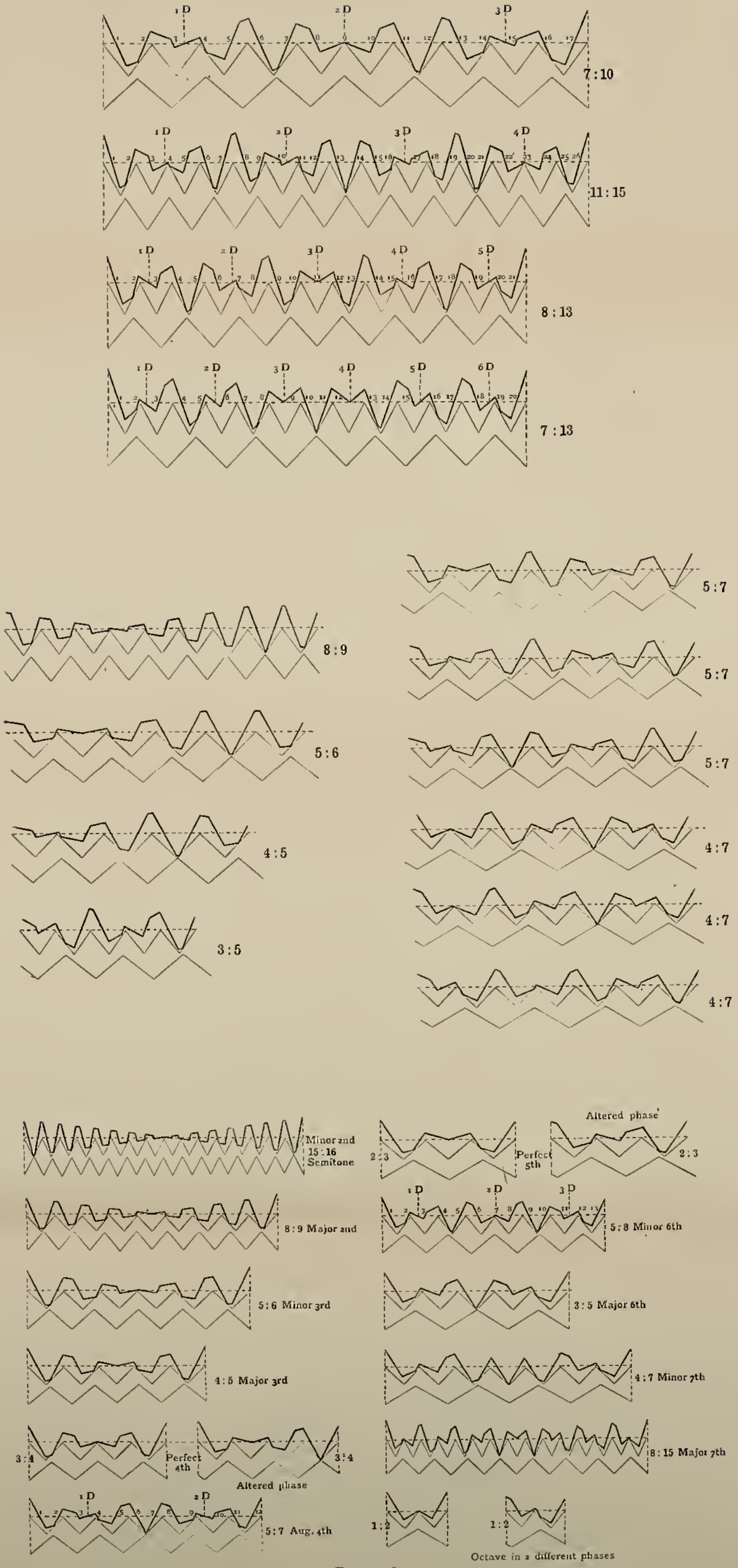
[10] Prof. Wm. Rutherford. *Brit. Med. Journ.* 1898. II. p. 353.

[11] Prof. Max. Meyer, *An Introduction to the Mechanism of the Inner Ear* (University of Missouri Studies). Columbia, 1907.

[12] Dr. O. Goebel, *Archives für Ohrenheilkunde.* 1912, Vol. 87, p. 42; 1913, Vol. 88, p. 89; 1913, Vol. 89, p. 280.

[13] Dr. Emile ter Kuile, *Pflüger's Archives.* 1900. Vol. 79, p. 146.

[14] Dr. Henry J. Watt, *The Psychology of Sound.* Cambridge University Press, 1917.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Minor 2nd
15 : 16
Semitone
2 : 3
Perfect
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Altered phase
2 : 3
8 : 9 Major 2nd
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3 D
5 : 8 Minor 6th
5 : 6 Minor 3rd
3 : 5 Major 6th
4 : 5 Major 3rd
4 : 7 Minor 7th
3 : 4
Perfect
4th
3 : 4
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8 : 15 Major 7th
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5 : 7 Aug. 4th
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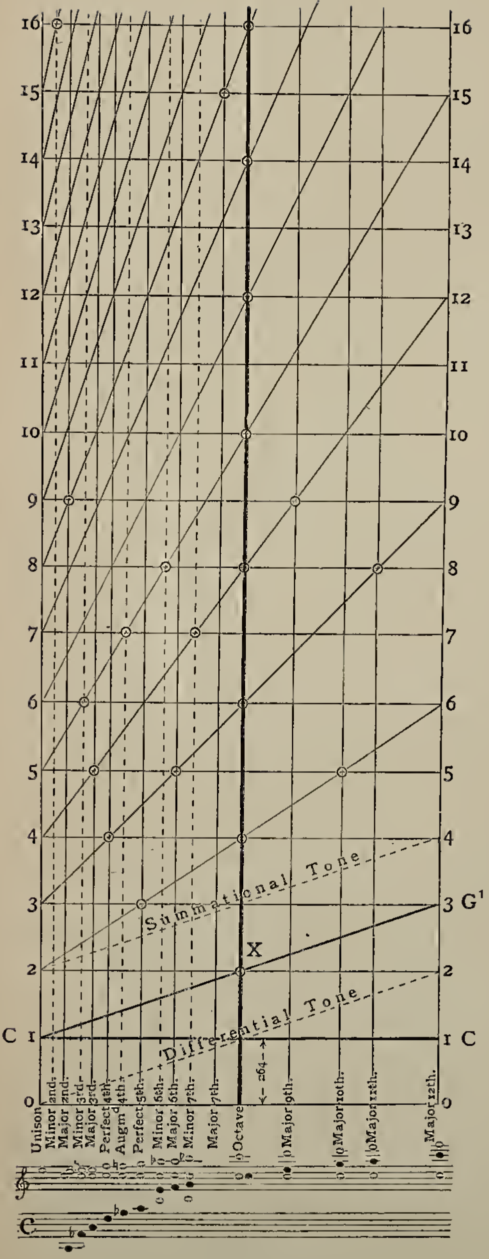
Octave in 2 different phases

PLATE I.



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Differential Tone
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Unison
Minor 2nd.
Major 2nd.
Minor 3rd.
Major 3rd.
Perfect 4th.
Augmd 4th.
Perfect 5th.
Minor 6th.
Major 6th.
Minor 7th.
Major 7th.
Octave
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Major 10th.
Major 11th.
Major 12th.

PLATE II.

Fig. 1
ELEVATION

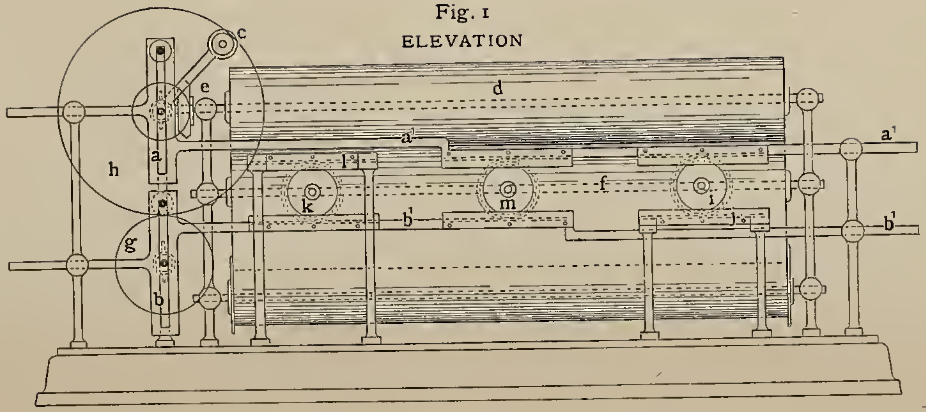


Fig. 2
END VIEW

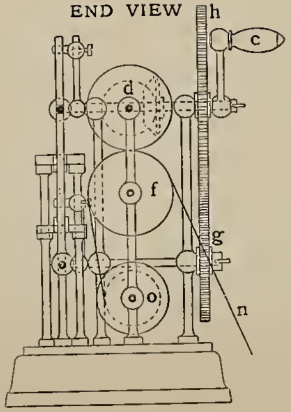


Fig. 3
PLAN

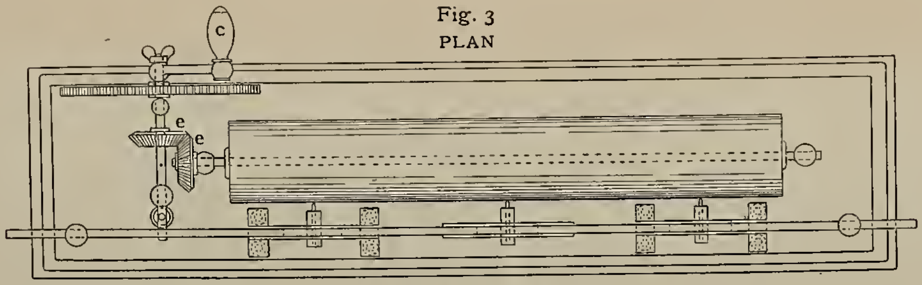
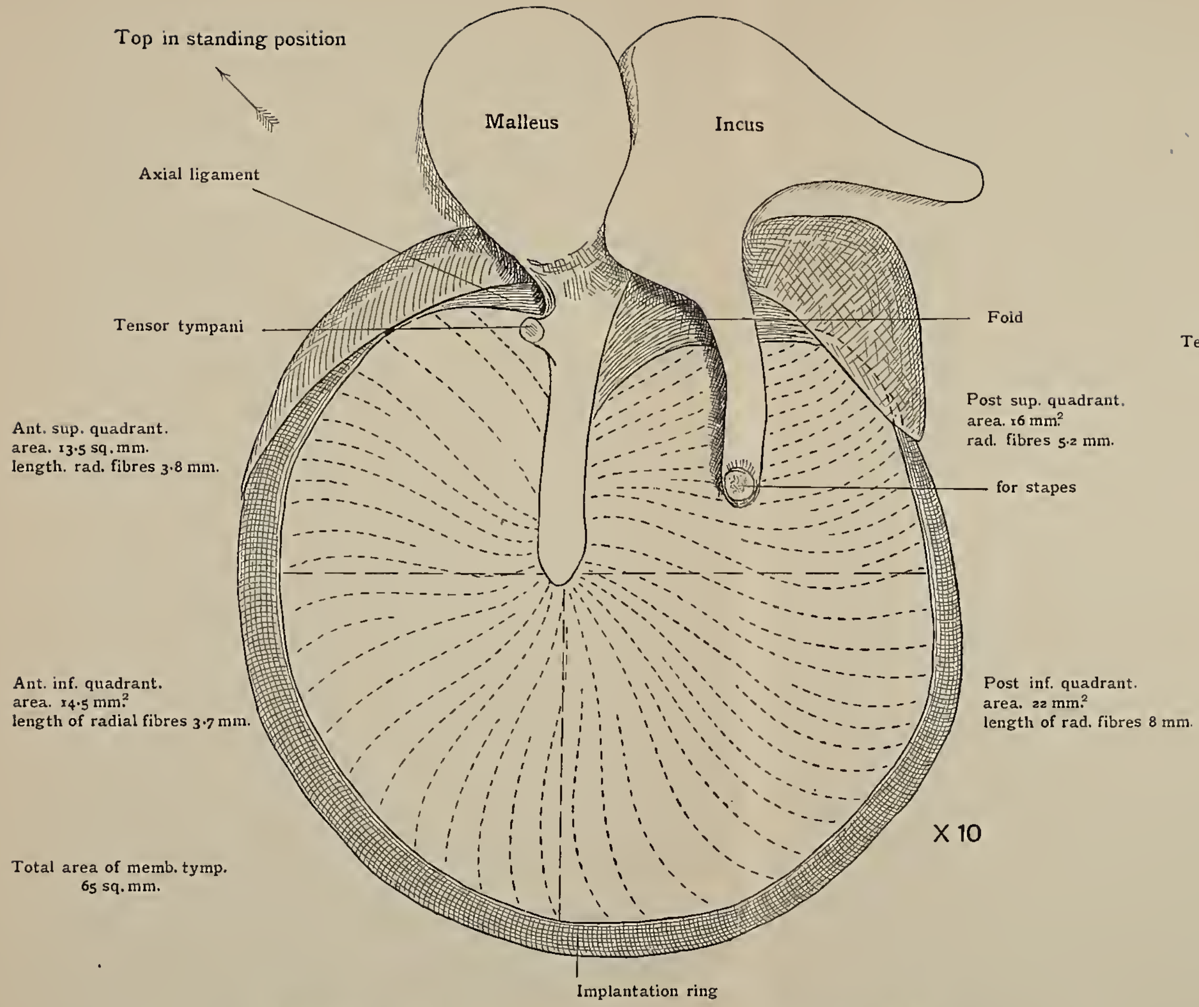
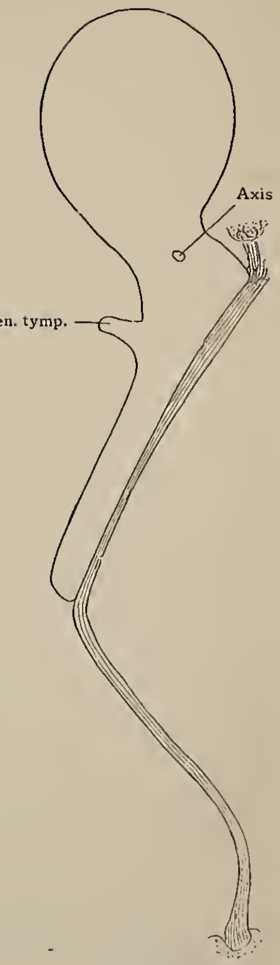
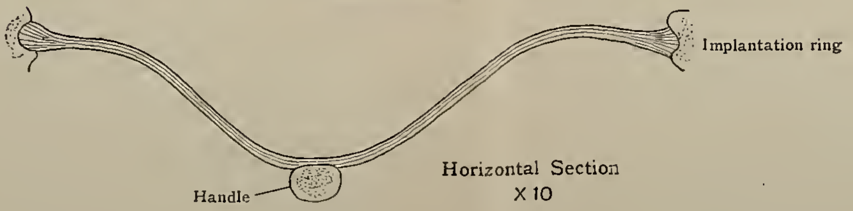


PLATE III.





Vertical Section
X 10



Horizontal Section
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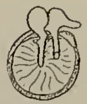


Natural size

KEITH

PLATE IV.

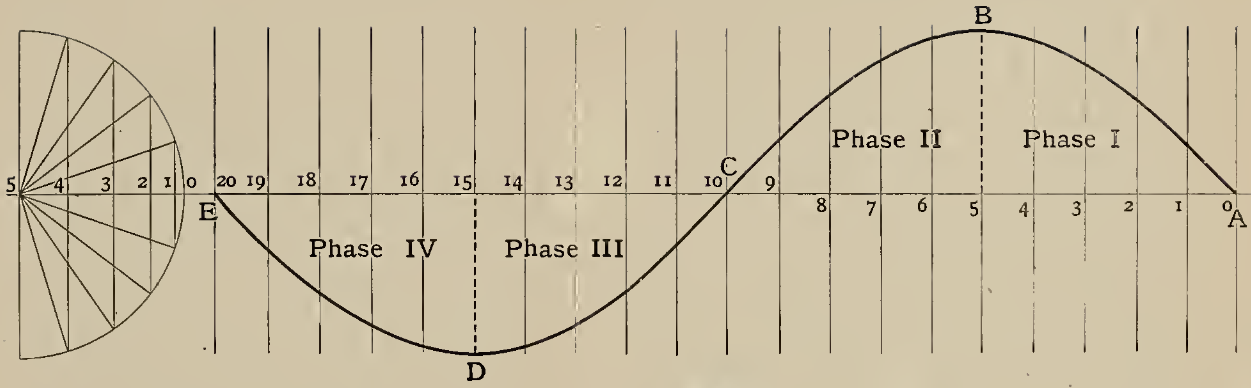
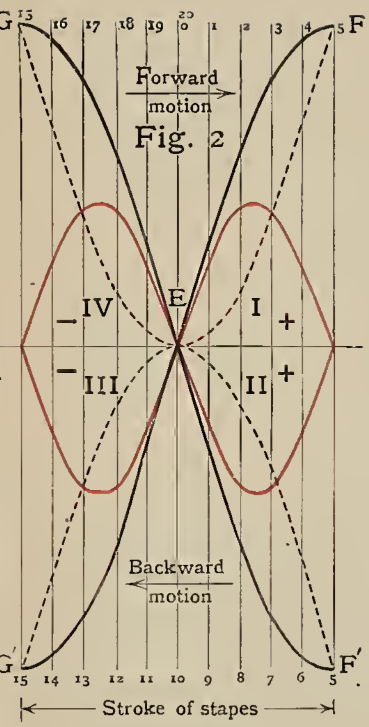


Fig. 1



Air wave same pitch as above but ½ the amplitude

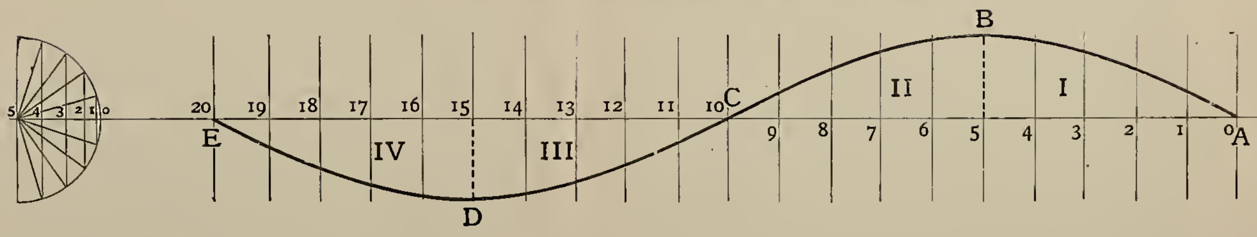


Fig. 3

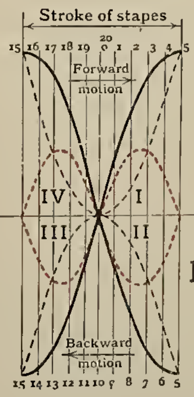
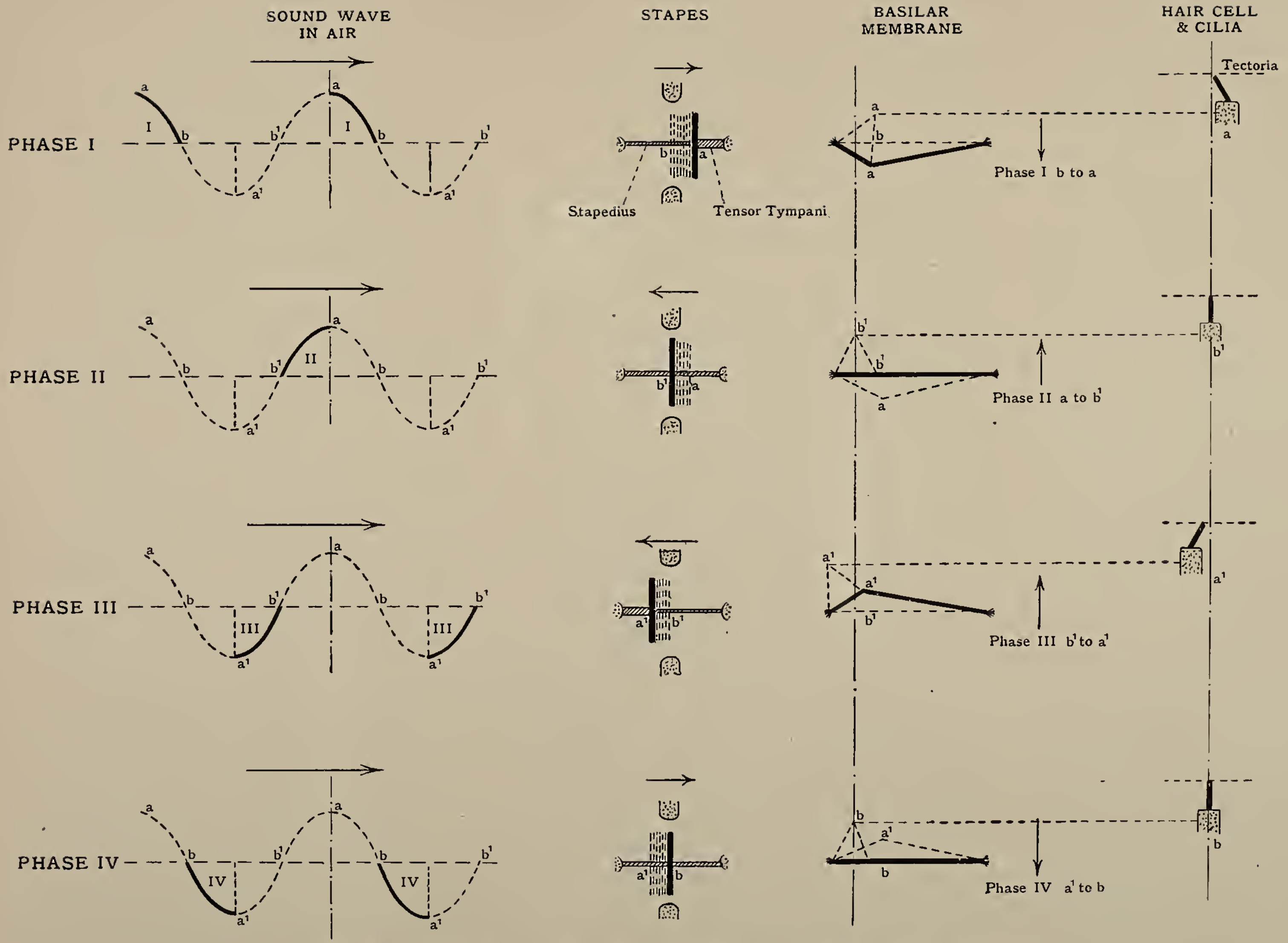


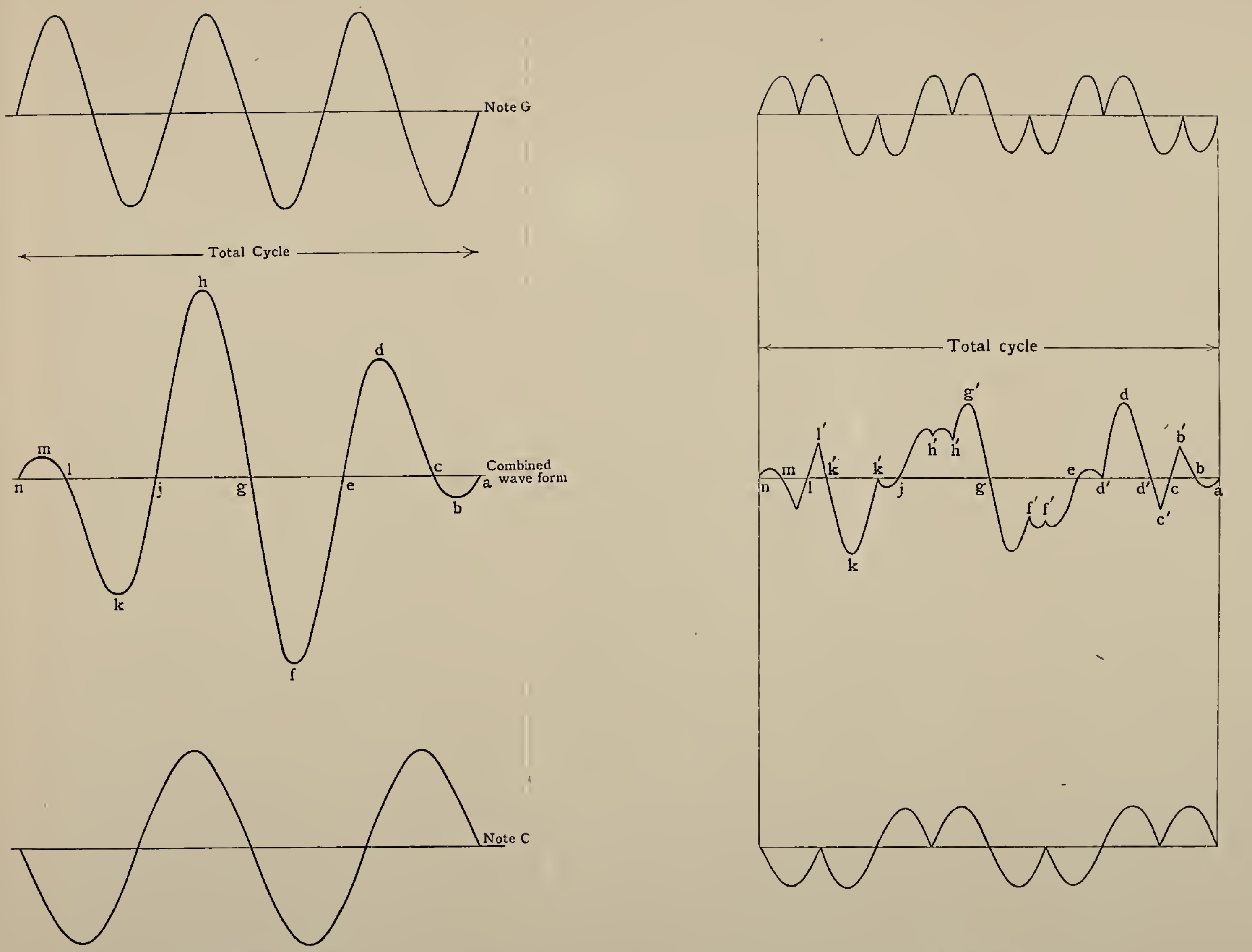
Fig. 4

Plate V.



NOTE. The Tensor Tympani and Stapedius muscles act on the ossicles in the middle ear but the effect in pulling the stapes inwards and outwards is the same as though they were attached to the stapes in the way indicated in this diagram.

PLATE VI.



Wave Forms in Air.

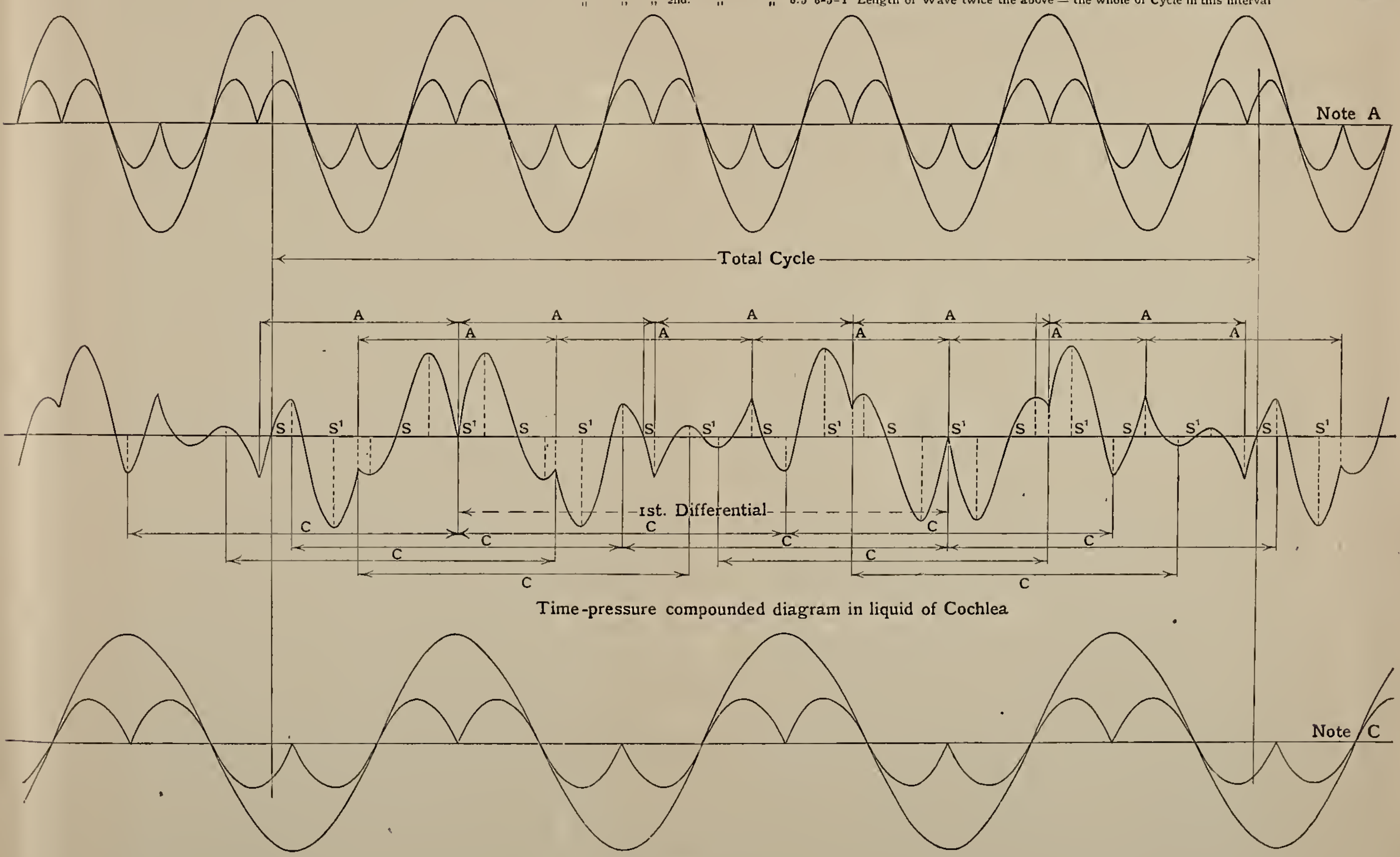
Wave Forms in Fluid.

Diagram showing modification of time-pressure of wave form when passed into the fluid of the cochlea.

Plate VII.

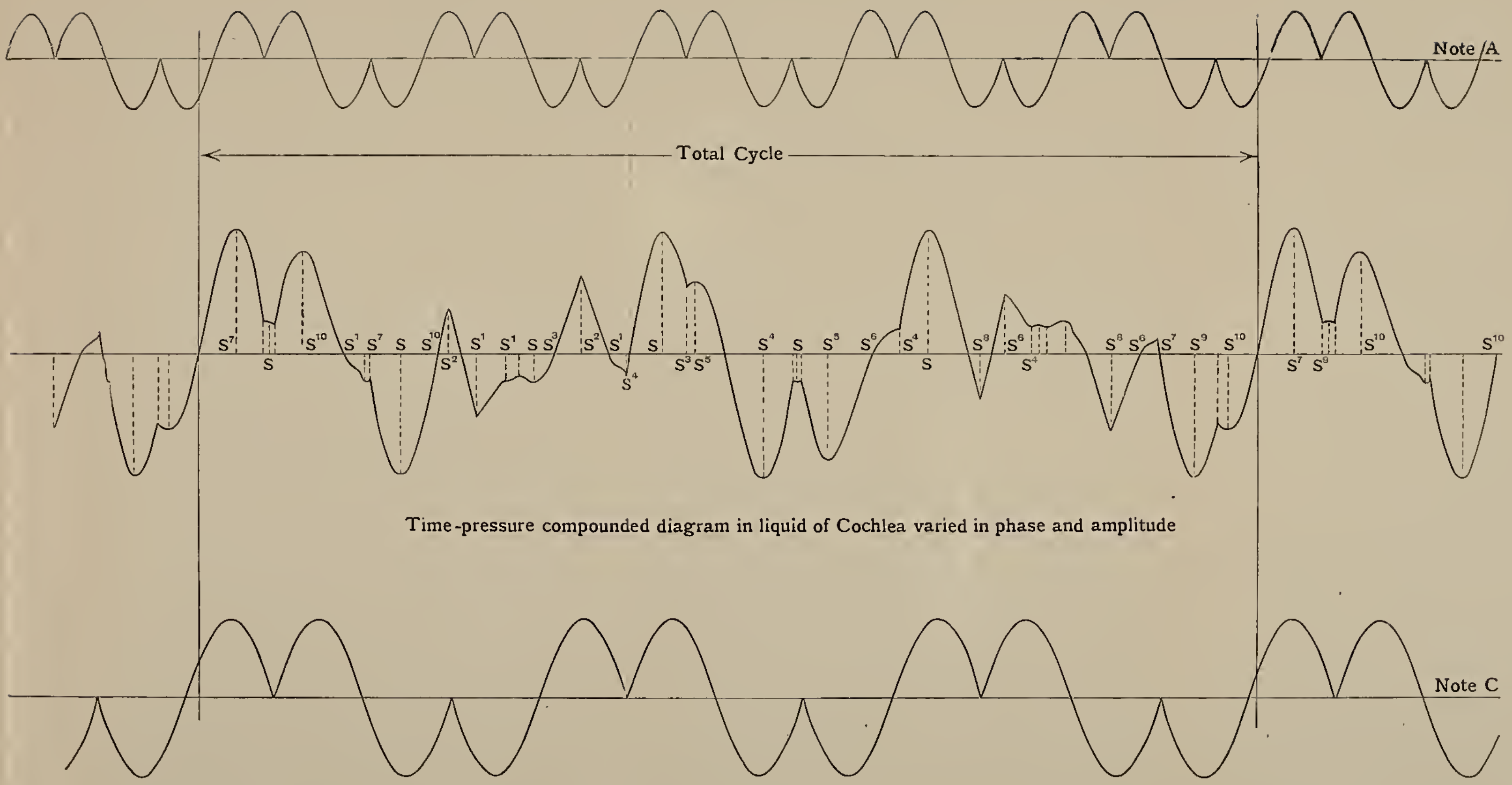
RATIO 3:5 MAJOR SIXTH
EQUAL AMPLITUDE PHASES STARTING TOGETHER

Wave length of "A" ⊢——⊣ 1/5 of the length of Cycle
" " " "C" ⊢——⊣ 1/3 of the length of Cycle
" " " Summational Tone 1/8 of Cycle ⊢——⊣ 1/8 of the length of Cycle
" " " 1st. Differential Tone 3:5 5-3=2 ⊢——⊣ 1/2 of Cycle in this interval
" " " 2nd. " " 6:5 6-5=1 Length of Wave twice the above = the whole of Cycle in this interval



Time-pressure compounded diagram in liquid of Cochlea

PLATE VIII.



Time-pressure compounded diagram in liquid of Cochlea varied in phase and amplitude

RATIO 3:5 MAJOR SIXTH C A
AMPLITUDE 8:5
HIGH NOTE PHASE ALTERED 1/7 OF CYCLE

Wave length of "A" 1/5 of the length of Cycle
" " " "C" 1/3 of the length of Cycle
" " " Summational Tone = 1/8 of Cycle 1/8 of the length of Cycle
" " " 1st. Differential Tone 3:5 5-3=2 1/2 length of Cycle in this interval
" " " 2nd. " " 6:5 6-5=1 = Length of Cycle or twice that of 1st. Differential in this interval

PLATE IX.

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